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community of lake Malawi/Niassa, Central Africa

Key words: Demersal fish, trophic model, sustainability, artisanal fisheries, taxonomy

COORDINATOR

UNIVERSITY OF DUBLIN DEPT ZOOLOGY TRINITY COLLEGE DUBLIN 2 IRELAND	DR. IRVINE, KENNETH E-M: kirvine@ted.ie TEL: 353-1-6081926 FAX: 353-1-6778094 Partner abbreviation: UDTC.DZ
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CONTRACTORS

UNIVERSITY OF DUBLIN DEPT ZOOLOGY TRINITY COLLEGE DUBLIN 2 IRELAND	DR. IRVINE, KENNETH E-M: kirvine@ted.ie TEL: 353-1-6081926 FAX: 353-1-6778094 Partner abbreviation: UDTC.DZ
KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPEN VAUTIERSTRAAT 29 B-1000 BRUSSEL BELGIUM	DR. MARTENS, KOEN E-M: Koen.Martens@naturalsciences.be TEL: 32-2-62 74 315 FAX: 32-2-64 64 433 Partner abbreviation: IRSNB.FBL
DEPARTMENT OF FISHERIES FISHERIES RESEARCH UNIT PO BOX 593 LILONGWE MALAWI	MR. MAPILA, S.A. E-M: sadcfish@malawi.net TEL: 265-721766 FAX: 264-721117 Partner abbreviation: MNRMW.FD.FRL
MUSEUM VOOR MIDDEN-AFRIKA B-3080 TERVUREN BELGIUM	DR. SNOEKS, JOS E-M: jsnoeks@africamuseum.be TEL: 32 2 7695628 FAX: 32 2 767 0242 Partner abbreviation: MRAC.LI
UNIVERSITY OF HULL SCHOOL OF BIOLOGICAL SCIENCES COTTINGHAM ROAD HU6 7RX HULL ENGLAND	PROF. CARVALHO, GARY E-M: g.r.carvalho@biosci.hull.ac.uk TEL: 44-1482-465540 FAX: 44-1482-465458 Partner abbreviation: UHULL.DBS.FG
UNIVERSITY OF EAST ANGLIA OVERSEAS DEVELOPMENT GROUP SCHOOL OF DEVELOPMENT STUDIES NR4 7TJ NORWICH ENGLAND	DR. ALLISON, EDDIE E-M: E.Allison@uea.ac.uk TEL: 44-1603-593724 FAX: 44-1603-505258 Partner abbreviation: UEANG.ODG

CONTRACTORS (continued)

UNIVERSITY OF SOUTHAMPTON SCHOOL OF BIOLOGICAL SCIENCES UNIVERSITY OF SOUTHAMPTON BASSETT CRESCENT EAST SOUTHAMPTON SO16 7PX ENGLAND, UK	PROF TURNER, GEORGE E-M: gft@soton.ac.uk TEL: 44-1703- 593217/4793 Fax- 44-1703 594269/4793 Partner abbreviation:USOU.DBE
UNIVERSITY OF MALAWI CHANCELLOR COLLEGE PO BOX 278 ZOMBA MALAWI	DR. AMBALI, AGGREY E-M: Ambali@unima.wn.apc.org TEL: 265-522622 FAX: 265-52270 Partner abbreviation: UMW.DB
MINISTRY OF NATURAL RESOURCES AND THE ENVIRONMENT TANZANIAN FISHERIES RESEARCH INSTITUTE PO BOX 9750 DAR ES SALAAM TANZANIA	PROF. BWATHONDI, PHILLIP O.J. E-M: Bwathondi@hotmail.com TEL: 255-51-650043/6 FAX: 255-52-650043 Partner abbreviation: TANZ.FRI

Abstract

The main objectives of the project were to:

- Provide trophic models to quantify energy flows through the demersal fish community and the food web that supports it in order to understand the principal components of the food web and to detect the main ecological effects of disturbance, such as increased fishing activity, on it; and
- Determine the existing fishing pressure on the demersal fish community through analysis of collected statistics in Malawi and Tanzania and to evaluate the accuracy of those statistics through calibration studies.

The project has advanced considerably the knowledge of fish and invertebrate taxonomy, provided a quantified description of food web dynamics affecting the demersal fish community and, for the first time, quantified artisanal fisheries activities along the coast of Tanzania. Supplementary novel information was collected on artisanal fisheries in Mozambique and new analysis and studies done by the Dept of Fisheries of Malawi. The diversity of demersal fish is even higher than previously thought and it is clear that some taxonomic problems are acute. Morphometric and genetic studies showed that many non-*mbuna* species are not homogeneous in their morphology over their distribution range. Significant differences were found in microsatellite allele frequencies among populations of some abundant demersal fish, suggesting segregation of stocks. Supporting data for model development came from sampling of lower trophic categories such as invertebrates and bacteria, previous sampling programmes on the lake or, where necessary, literature derived figures. Updated guides to benthic invertebrates were produced.

Ecosystem modelling indicated that the main pathway for energy flow through the demersal fishery is through the consumption of copepods by demersal fish apparently migrating into the pelagic for feeding. The lakefly, *C. edulis*, provide a direct link between the demersal fish community and pelagic productivity but its importance is less than it is in the pelagic zone of the lake. By integrating the demersal and pelagic components of the Lake Malawi ecosystem into a single model, ecological efficiency of the lake appears to be much greater than previously supposed and the demersal fish community is able to directly utilise much of the pelagic production previously thought to be exported to detritus.

The lake contains a high proportion of trophically equivalent fish which could be important for maintenance of ecosystem function. Prudent exploitation of the fishery would maintain this diversity to provide a buffer against possible environmental change or trophic knock-on effects of high fishing pressure. It is, however, clear that current fishing practice in the south of the lake threatens both biodiversity and a sustainable fishery. There is a need for a reappraisal of fisheries management and, throughout the lake, continued support for development of monitoring and research programmes.

Summary of Final Report

The project comprised a consortium of six European and three African partners with, in addition, some limited participation from the Fisheries Institute Mozambique. The project comprised nine Tasks:

- Task 1, Programme planing and project coordination;
- Task 2, Primary photosynthetic and microbial production;
- Task 3, Diversity, structure, seasonality and production of invertebrate communities;
- Task 4, Fish taxonomy;
- Task 5, Fishery assessment and growth rates of demersal fish;
- Task 6, Fish diet analysis;
- Task 7, Stable isotope work;
- Task 8 Trophic modeling; and
- Task 9, Conclusions

These tasks were divided into three categories of, respectively, taxonomy and genetics, fisheries assessment and trophic modelling. Partner collaboration involved overlaps of skills required to fulfill the project objectives. The project was coordinated by the Trinity College, University of Dublin, Ireland.

A regional base was established at Senga Bay in Malawi, and the first six months was spent largely with the establishment of an infrastructure within which the project could operate. In August of that year the project established a base in Senga Bay Malawi. The project began work in the region in September 1998, with the first extensive research cruise. Subsequent extensive cruises were done in March 1999 and September 1999 through the hire of the research vessel, R/V USIPA. Interim collaborative cruises were done in collaboration with a SADC/GEF Biodiversity project and with the Malawi Fisheries Research Unit.

During the open water cruises, trawling of fish was done down to 125 m depth. Deeper trawling proved impossible owing to mechanical limitations. Attempts to modify the trawl to enable deeper samples of fish to be collected were unsuccessful. Nevertheless, the project was successful in collecting data on fish distribution from a significant portion of the demersal zone and from different locations off the coasts of Malawi, Mozambique and Tanzania. During the lake cruises, samples from the benthos were collected down to the oxygen boundary at >200 m depth.

Rates of bacterial production, based on incorporation of labelled nucleotide bases, were similar in Lake Malawi as those found in Lake Tanganyika and appear substantially higher than in marine systems with comparable levels of primary production. The work suggested that depth integrated rates of bacterial production may be comparable with primary production at certain times of the year. Bacterial rates based on tritiated thymidine uptake compared well with direct observations of bacterial cell and biomass increases in June but were much lower than direct observations of increases in biomass in January.

Diversity and densities of invertebrates declined with increasing depth. Molluscs and insects disappeared very quickly; present at 10 m but completely absent from sediment samples at 30 m. Other taxa were found at depths of 125 m. Bivalves, nematodes and chironomids were found in relatively high numbers, up to 2000 individuals m⁻², but all were completely absent in the sample collected from 200 m where only few *Chaoborus* larvae were found. Disappearance of most benthic invertebrates is likely to be related to oxygen availability. At depths below 175 m the water overlying the sediments can go anoxic and at depths > 130 m the concentration of oxygen is often < 2 mg O₂ l⁻¹. *C. edulis* does not appear to be as abundant in the demersal sediment as previously thought. High fish populations indicated by acoustic signals near the oxic-anoxic boundary of the demersal continue, therefore, to provide a conundrum.

Two invertebrate groups of particular interest for species diversity in the African Great Lakes have been the molluscs and the ostracods. The mollusc fauna of Lake Malawi and associated water bodies is now taxonomically revised. In total, 38 mollusc species in 14 genera have been reported from Lake Malawi; 55% of which are endemic to the lake and/or associated water bodies. Dredge samples from the S.E. Arm of the lake showed that the mollusc fauna of Lake Malawi is reasonably well-known compared with the ostracods. Where previously only 20 species of ostracod had been reported (mostly from associated water bodies), 40 more, all lacustrine, were found in the course of our work. Of these, at least 35 are new species. Number of ostracod species per sample was also high, ranging between 8 and 14. The project produced a generic key to the invertebrates of Lake Malawi for use by non-specialist biologists.

It is now apparent that the diversity of the fish fauna is even greater than previously thought. The project, nevertheless, made significant progress with solving some of the taxonomic difficulties posed by the species-rich demersal community of the lake. In particular, there was good progress separating species of the deep water *Lethrinops* complex. These are an important component of the demersal fish community, whose taxonomy hereto has been poorly understood.

Standard methods using the study of colour patterns and morphometrics combined with univariate and multivariate data analyses (Snoeks, 1994, 1999) were used for cichlid taxonomy. For each individual specimen analysed, some 23 measurements and 18 meristics were recorded and complemented with several qualitative observations. Multivariate techniques used were primarily Principal Component Analyses (PCA); non-parametric, distribution-free tests such as the Mann-Whitney U test were used for univariate comparison. Early in the project a priority list of groups for special study was agreed among project partners. These focused on economically and ecologically important species, particularly *Lethrinops*, *Mylochromis anaphyrmus*, *Copadichromis virginalis* complex and *Placidochromis* sp. 'platyrhynchos'.

This work included an important genetic component to help separate species complexes and help understand population interchange among stocks of some important demersal species. Other important studies were on diversity of population structures and phylogenetic analysis of many of the common demersal cichlid fish. Genetic work has been done through collections of demersal fish that were obtained by the dedicated cruises of the project and by the analysis of seasonal artisanal

catches. The project found no evidence for substantial genetic differences between samples of *P. platyrhynchus*, although some small but significant differences between samples suggest that levels of gene flow (i.e migration) between areas is not extensive. In contrast, significant differences were observed among the samples of *Lethrinops* sp. 'deep-water albus', both within and between geographically distinct shelf areas, with by far the most distinct samples coming from the area near Nkhotakota. The results for *L.* sp. 'deep-water albus' are consistent with restricted migration between areas and/or the presence of cryptic taxa (species). Microsatellite DNA markers revealed small but significant levels of population substructuring over all studied *Copadichromis* sp. kayose populations ($F_{ST}=0.004$, $P=0.002$; $R_{ST}=0.019$, $P<0.00001$) and related species. This structuring was low and over a much larger geographic scale when compared with previously published studies of the mbuna (rock-dwelling species), but greater than that found in pelagic cichlid species inhabiting Lake Malawi. In many respects the demersal habitat of Lake Malawi bears more resemblance to a marine environment than to many freshwater habitats. The distances between populations can be quite large, and there are no obvious physical barriers constraining migration. The lack of a pelagic dispersal phase and a low fecundity may allow substructuring to occur at much smaller geographic scales (<300km) than are typically found in marine demersal habitats. The presence of low levels of population substructuring is likely to have implications for fisheries practices on the lake. At present, commercial trawling is concentrated over a limited area in the S.E. Arm. These data suggest that overfishing is unlikely to lead to the extinction of the population(s) of the species studied in this area, as migrants are likely to move in from surrounding areas. However, intense fishing pressure could still lead to significant reductions in population sizes and, as indicated by the modeling work, impact on the ability of the lake's ecosystem resilience to future changes affecting the fisheries.

The genetic distribution of commercially exploited cichlids of the inshore artisanal fisheries of the lake using *Taeniolethrinops praeorbitalis* as a model, showed that populations have high allelic diversity, with no significant differences found in allelic diversity between Mangochi and Nkhota-kota populations, but with considerable local genetic diversity in those populations, as indicated by a high proportion of rare alleles. Although the Mangochi populations generally experience a higher exploitation pressure, their allelic diversity was not significantly different from that of Nkhota-kota populations.

Despite challenging logistical problems, the project made significant progress with a programme of artisanal data collection in Tanzania and, in collaboration with the SADC/GEF Biodiversity Project, the University of Waterloo, Canada and the Government of Mozambique, in some inshore waters in Mozambique. The demonstration of the feasibility of this is important as the artisanal fishery represents the most intense impact on fish stocks in the lake. Frame surveys, to estimate the fleet size and composition of the artisanal fishery providing important indicators of the health of the fishery and are essential to provide raising factors to estimate fishery effort, when combined with catch per unit effort (CPUE) data.

The Malawian sector of the lake was found to have been well covered by the existing frame surveys which have been run since 1976. However, economic contingencies had led to the suspension of the survey for several years. Five research programmes:

artisanal gear selectivity, gillnet selectivity, population parameters, frame survey and trawl selectivity, were agreed between the Malawian Fisheries Department and supported by the project. The survey and a sampling programme covered the coastline of Malawi territory, incorporating the fishing districts of Mangochi, Salima, Nkhosakota, Nkhosakota Bay and Karonga. A total of five lake-wide surveys were conducted between 1998 and 1999 in collaboration with collaborative with the GTZ-sponsored National Aquatic Resource Management Program (NARMAP).

The number of fishermen, fishing gears (in particular small mesh gears) and vessels has increased enormously in almost all the districts in recent years with a use of a variety of gears. A high degree of species overlap was found in the catches. Catch composition of all gears sampled was multi-species and a total of 178 fish species were identified in the small-scale fishery during the surveys. The most commonly caught species from most of the gears were *Lenthrinops* spp. *Copadichromis* spp., *Dimidiochromis* spp. and the large catfishes (*Bagrus* and *Bathyclarias* spp.). Most of the gears except the gillnets land many small fish mainly juveniles <3.5 cm TL. Sizeable fish > 7.5 cm TL were landed from gillnets. Total catches for most gear types were low in inshore waters. Consequently fishers travel further to offshore waters where the catches are higher but, nevertheless, fishers using boats with engines are relatively few as opposed to fishers using boats without engines and dugout canoes are common. More than 61 species were recorded in most fisheries, the exception being large meshed gill nets (GN4) and longlines. The number of species identified in catches from the different gears ranged from 8 species in the large meshed gillnet fishery to 142 species recorded in the chilimira net fishery. There were considerable differences in the number of species identified in the small-scale fishery in each area. However, since the numbers and types of gears sampled in each area were different, this variation may not be a reliable indication of diversity.

Owing to declining catches in the artisanal fisheries of Malawi, most fishers have modified the fishing methodology, which has resulted into modification of the gear itself or fishing pattern. This was evident in most districts and includes operating gillnets as active, rather than passive gears, and reducing gill net mesh sizes, in some cases to 2-inches which is illegal. Such gillnets target utaka which is mostly caught using the open water seines (chirimila). In Karonga, gillnets have hooks fixed on the foot ropes and head ropes. Light attraction is also playing a major role in most fisheries in the fishing districts of Malawi.

The findings of the project strongly indicates that the southeast arm, where most of the work was based, is under severe fishing pressure that requires sustainable management strategies to be placed immediately to minimise further environmental deterioration. Virtually all the depth ranges seem to be exploited at present and there is a proliferation of small meshed gear fisheries in the area. There is an urgent need for a reappraisal of fisheries management and survey techniques in order to support a future sustainable fishery.

As far as could be determined, no frame survey had previously been carried out on the Tanzanian sector of the lake. The project designed and carried out a series of frame surveys on the Tanzanian shores. The results showed that both the number of fishermen, fishing craft and gear change with seasons. For Kyela district which is mainly a flood plain, access by fishermen to the lake becomes difficult as the coastal

area is mostly swampy. There is also a dynamic change of livelihoods as most people engage in paddy farming. The coastal area for Ludewa district is characterized by slopes of Mt. Livingstone and therefore farming is mainly subsistence, and in most places practiced by women. Lake Nyasa fish production is higher during the rainy season than during the dry season, with an importance of cyprinid *Opsaridium* species, Mpasa and Mbelele, that migrate into the rivers. There is a higher concentration of fishermen in the river mouths during the rainy months compared with the dry seasons. At the time the project started there was no governmental fisheries infrastructure on the Mozambican side of the lake, and very little fishing activity. This situation only improved marginally by the time of cessation of our fieldwork in 2000. However, in 2000 we did manage to advise on the conduct of a full frame survey of the Mozambican shore in collaboration with the GEF project.

The combined Lake Malawi fisheries exploit in excess of 300 species of fish which exhibit a broad range of life history traits that may respond in significantly different ways to fishing pressure. A single species management approach is inappropriate and many of the multi-species, multi-gear and ecosystem approaches are likely to prove too costly. While the choice of management strategy is not obvious, it is clear that further development of an effective assessment and management strategy is required with some urgency. We suggest that:

1. Management objectives must be clarified – is the fishery to be managed principally for maximum economic yield, for maximum biomass yield, for sustaining livelihoods for as many fisherfolk as possible, for conservation of diversity, or for a combination of these?;
2. The level of available management resources (human and economic) must be determined;
3. Potential options for management strategies and their data requirements and costs should be determined; and
4. A management strategy should be chosen which can meet the management objectives while remaining within the limits of the economic and human resources available for its implementation.

Diet analysis, supported by stable isotope work, showed ten main trophic guilds among the demersal fish community, ranging across three-four trophic levels. An additional guild was formed to incorporate those shallow water species not often encountered in the demersal trawls which were reported in the literature as feeding on epilithic algae and macrophytes. The mean trophic level of the demersal fish community for all depths and sample areas, pooled and weighted by their respective areas of lakebed coverage, was 3.18 with the bulk of biomass (58%) concentrated at trophic level 3.0. Mean trophic values were highly significantly influenced by water depth and sample location (ANOVA, 5 depth bands, 8 locations, 356 samples). The main influence of depth was realised in the shallow water where mean trophic values in the 0-20m depth band were significantly lower than at all other depths (Tukey: $p < 0.001$).

For many taxa there appears a high proportion of trophic-equivalence within the Lake Malawi demersal fish community. If the ceiling of available energy (resource limitation) is the main limiting factor in community structure, then any particular functional community structure might comprise an array of species with similar

adaptations. If this is true, variety within the overall community composition comprises a number of functional analogues which must be maintained by spatial variability or perhaps behavioural mechanisms operating across species complements. While subtle mechanisms may be at play to retain this position and support the unusually high species diversity of the lake, the results suggest that elimination of species will result in subsequent replacement by functional analogues. However, such functional analogues could also be highly important for the maintenance of ecosystem function through provision of a buffer against environmental change. Loss of these species could be highly damaging to the long-term resilience and ecological integrity of the community and, therefore, the viability of the fishery.

The proposed role of lakeflies (*C. edulis*) larvae in the ecosystem has been somewhat clarified. Allison *et al.* (1995) showed that *C. edulis* was a more important food source to the pelagic fish community than originally suggested by Degnbol (1993), and went on to propose that demersal fish might also rely on consumption of *C. edulis* larvae. The integration of the demersal and pelagic systems within the current model shows that approximately 50% of *C. edulis* production is directly consumed by pelagic fish, and a further 4% by demersal fish. The remaining 46% of production either flows to detritus, where a certain proportion will be recycled through detritivores, or leaves the system through dispersal as flying adults (some of which return to the lake and are consumed by surface-feeding catfish).

In the demersal zone the role of *C. edulis* is less than that in the pelagic. System modelling suggested that although *C. edulis* does indeed provide a direct link between the demersal fish community and pelagic productivity, the main pathway for energy flow in the demersal domain is through the consumption of copepods by demersal fish apparently migrating into the pelagic for feeding. Integrating the demersal and pelagic components of the Lake Malawi ecosystem into indicates that the lake is much more efficient than previously supposed (e.g. Hecky, 1984) as the demersal fish community is able to directly utilise much of the pelagic production previously thought to be exported to detritus. In summary, the demersal system appears to rely most heavily on biomass imported from the pelagic through consumption of copepods by fish migrating vertically to feed in the pelagic, and through a fall out of diatoms which are consumed by fish sifting them from the sediment ooze.

Scenario modelling indicated that current fishing levels will lead to trophic change, as well as species change. Increasing those levels of fishing (as is likely under the current pressure on stocks and the lack of enforcement capacity) will cause further change in both species composition and trophic structure, although total fish yields may continue to increase, particularly if fishing is expanded into areas where there is currently a low level of fishing effort (the deep water demersal and offshore pelagic zones).

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Consolidated Scientific Report

Objectives

The main project objectives were to:

- identify the main fish species that inhabit the demersal zone of the lake and resolve taxonomic difficulties using morphometric techniques, supported by genetic ones;
- determine the trophic structure of the demersal fish community and identify important bacterial, photosynthetic and invertebrate components that support the fish community.
- provide trophic models that will quantify energy flows through the demersal fish community and the food web that supports it in order to understand the principal components of the food web and to detect the main ecological effects of disturbance, such as increased fishing activity, on it.
- to assess existing fishing pressure on the demersal fish community through analysis of collected statistics in Malawi and Tanzania and through new survey work.

The project was designed to provide information to assist with the sustainable management of fish stocks and provide recommendations for an integrated approach to the collection of fishery statistics throughout the lake. The project results will assist in the lake-wide management of the lake's ecosystem and strengthen the understanding of both biodiversity and fisheries.

The project comprised a consortium of six European and three African partners with, in addition, some limited participation from the Fisheries Institute Mozambique. A integrated network was established among project partners in order to complete nine defined *Tasks*. Partner collaboration involved overlaps of skills required to fulfill the project objectives which were broadly divided into: taxonomy and genetics; fisheries assessment; and trophic modelling.

Activities, results and problems

Task 1. Programme planning and project coordination. Lead partner: UDTC.DZ. Other partners: All.

Activities and results

A regional base was established at Senga Bay in Malawi, and the first six months was spent largely with the establishment of an infrastructure within which the project could operate. In August of that year the project established a base in Senga Bay Malawi. The project began work in the region in September 1998, with the first extensive research cruise. Subsequent extensive cruises were done in March 1999 and September 1999 through the hire of the research vessel, R/V USIPA. Interim collaborative cruises were done in collaboration with a SADC/GEF Lake Malawi/Nyasa Biodiversity Conservation Project and with the Malawi Fisheries Research Unit.

Planning of research cruises was done in consultation with project partners and the SADC/GEF lake Malawi/Nyassa Biodiversity Project. Activities of partners were agreed prior to the project and through email discussions and project meetings. Logistics in Malawi, and management of artisanal work in Tanzania and Mozambique 1999-2000, were managed by the research worker employed in collaboration between UEANG.ODG and USOU.DBE. Regular, at least monthly and often daily, communications were maintained between EC staff in the region and the project coordinator

Problems encountered

Overall, the logistics of the project were implemented successfully. It is inevitable that in the working conditions encountered by the project, problems with electricity supply, telecommunications, dependency on a research vessel at specified times and general difficulties of transport among the project base and work stations elsewhere in Malawi, Tanzania and Mozambique would arise. The project personnel resolved most problems. Some anticipated sampling time was lost owing to mechanical failure of the R/V Usipa and, towards the end of the field period a difficulty over insurance of the boat prevented the final lake cruise programme.

Task 2: Primary photosynthetic and microbial production (Lead partner: UDTC.DZ)

Activities and results

Owing mainly to logistical difficulties there is very limited data on photosynthesis in the lake. Estimates (Guildford et al 1999), that come from the final report of the SADC/GEF Biodiversity Project (Bootsma and Hecky, 1999), are of average open-water photosynthesis rates of $1.75 \text{ mg C m}^{-3} \text{ hr}^{-1}$ in the upper layer of a station in the south-west arm the lake during 1997. Guildford *et al.* (1999) also reported estimates of benthic concentrations of chlorophyll *a*, sampled in November 1996, that ranged from $75\text{-}176 \text{ } \mu\text{g l}^{-1}$, $58\text{-}122 \text{ } \mu\text{g l}^{-1}$ and $70\text{-}94 \text{ } \mu\text{g l}^{-1}$ at, respectively, 2m, 5m and 10m depth. Bacterial productivity in the lake and its relationship with benthic invertebrate communities was achieved through a subcontract to the University of Waterloo, Canada. This involved estimation of bacterial activity at a number of depth profiles in the southern half of the lake. A full report on this work has already been submitted as a deliverable of the project and only summary points are included here. Mean pelagic bacterial production rates ranged from 4.8 mg C m^{-3} in the upper water column to 12.5 mg C m^{-3} in the lower water. Bacterial biomass correlated with chlorophyll *a* concentration but bacterial production did not correlate with bacterial biomass or chlorophyll *a* because highest rates of bacterial production occur in the lower water column.

While bacterial production rates, based on tritiated thymidine uptake, compared well with direct observations of bacterial cell and biomass increases in June, they were much lower than direct observations of increases in biomass in January. In January, it appears that there was a different bacterial community, in which rod-shaped bacteria were the most actively growing component. Rates of bacterial production were similar to those of Lakes Tanganyika. High rates of aerobic heterotrophic growth in the deep waters may lead to high rates of oxygen consumption in the African Great Lakes. Integral rates of bacterial production in Malawi/Niassa were similar to primary production at certain times of the year if the whole water column is

considered. More research with higher frequency of sampling and greater spatial coverage is required to determine the balance of autotrophy and heterotrophy in the lake.

Problems encountered

The results obtained from the bacterial work were new and important, but limited in their seasonal and spatial coverage. This was not unexpected but important to recognize that these are the first data on bacterial production rates from the lake and such samples take considerable effort to collect. Clearly, further spatial and temporal coverage would provide a more complete picture of the importance of bacterial production for the food web of the lake.

Task 3: Diversity, structure, seasonality and production of invertebrate communities. Lead partner: IRSNB.FBL. Other partners: UDTC.DZ.

Activities and results

This task involved the employment of an additional research worker employed for the first part of his contract by UDTC.DZ and for the second half by IRSNB.FBL. The project also benefited from involvement of the input of Dr Kelly West, an expert on African Great Lakes molluscs. Putative records of all non-insect invertebrate groups from Lake Malawi and associated waters were checked in the Zoological Record. From this collected literature, taxonomic lists of non-insect invertebrates recorded previously in or around the lake were compiled. Specialists then screened these lists for potential synonyms and obsolete nomenclature. During the open-water cruises of the project, benthic samples were collected from a range of depths and location using EKMAN, PETITE PONAR grabs and a benthic dredge. Samples from the benthos were collected down to the oxygen boundary at >200 m depth. Subsidiary samples were collected with a hand net in water <30 m using SCUBA. The latter proved quite ineffectual in collecting material from the generally soft substrata of the lake. The extant diversity of two groups (Mollusca and Ostracoda) was determined from a subset of these samples to test how representative the list of published records is. New taxa of Ostracoda were illustrated using Scanning Electron Microscopy. Based on the extant groups, a key to the major invertebrate groups was produced.

While numbers of benthic invertebrates varied with depth among taxa, there was an overall decline in both diversity and densities with increasing depth. Molluscs and insects disappeared very quickly; present at 10 m but completely absent from sediment samples at 30 m. Other taxa were found at depths of 125 m. Bivalves, nematodes and chironomids were found in relatively high abundance, of up to 2000 individuals m⁻², but all were completely absent in the sample collected from 200 m where only few *Chaoborus* larvae were found. Disappearance of most benthic invertebrates is likely to be related to oxygen availability. At depths below 175 m the water overlying the sediments can go anoxic and at depths > 130 m the concentration of oxygen is often < 2 mg O₂ l⁻¹. Benthic samples indicated a benthos of generally low abundance and a decline of both abundance and diversity with depth. The benthic invertebrates may be further restricted by the physical nature of the sediment and/or low supply of detrital food that, in the high temperatures of the lake, may be largely mineralised on its way from the productive euphotic to the deeper profundal zones. Apart from larvae of the lakefly *Chaoborus edulis*, no invertebrates were found below

the oxycline in the lake. *C. edulis* do not, however, appear to be as abundant in the demersal sediment as previously thought. High fish populations indicated by acoustic signals near the oxic-anoxic boundary of the demersal continue to provide a conundrum. Two groups of particular interest for species diversity in the African Great Lakes have been the molluscs and the ostracods.

Mollusc diversity

The mollusc fauna of Lake Malawi and associated water bodies is now taxonomically revised (West, 2001). In total, 38 mollusc species in 14 genera have thus far been reported from Lake Malawi; 55% of the species are endemic to the lake and/or associated water bodies. Molluscs were identified from several rich dredge samples from the S.E. Arm of the lake. Five gastropod species and 4 bivalve species were found. None of these species and genera were new. This indicates that the mollusc fauna of Lake Malawi is reasonably well-known, at least compared with smaller groups, such as ostracods.

Ostracod diversity

The diversity found was very high. Where previously only 20 species had been reported (mostly from associated water bodies), no less than 40 species, all lacustrine, can now be added to the list, bringing the total to 60. Of these, at least 35 are new species, more than half of which belong to at least two new genera; 62% of the species are endemic to the lake and surrounding waters. The main radiations are in Cypridopsinae (18 new species in at least one new genus), *Limnocythere s.l.* (10 new species in several genera, some possibly new), *Gomphocythere* (4 new species) and finally a new cypridid genus, tentatively placed in the Cyprinotinae (3 new species). The 6 *Chrissia* species are not endemic to the lake and moreover are mostly found from associated water bodies; they are not considered as a lacustrine species flock of this lake. Number of ostracod species per sample was also high, ranging between 8 and 14, but the number of shared species and similarity indices were low.

The project has produced a generic key to the invertebrates of Lake Malawi for use by non-specialist biologists.

Problems encountered

There were early difficulties with the collection and preservation of benthic invertebrates, but these were resolved by the second lake cruise in March 1999. However, despite the successful collection of invertebrates from the main cruises and agreement with the SADC/GEF Biodiversity Project for collection of benthic invertebrates in the SW arm at monthly collections sample processing proceeded at a slow pace. This, coupled with logistical difficulties, impinged on progress with estimation of invertebrate production rate and this work did not reach a satisfactory conclusion. The low abundance of *Chaoborus* larvae found in the grab samples was a surprise as previous work (Allison, Irvine & Thompson, 1996) suggested that the shallow benthos was an important refuge for the IV instar larvae. It may have been that the heavier PONAR, compared with the lighter EKMAN grab (used previously) may have displaced resting larvae with a pressure wave prior to hitting the sediment. However, EKMAN grabs also taken during the current project revealed low numbers of *Chaoborus* larvae.

Task 4. Fish taxonomy. Lead Partner MRAC.LI, supported with genetic work by IRSNB.FBL, UHULL.DBS.FG and UMW.DB.

Activities and results

During the open water cruises, trawling of fish was done down to 125 m depth and the project was successful in collecting data on fish distribution from a significant portion of the demersal zone and from different locations off the coasts of Malawi, Mozambique and Tanzania.

Standard methods using the study of colour patterns and morphometrics combined with univariate and multivariate data analyses (Snoeks, 1994, 1999) were used for cichlid taxonomy. For each individual specimen analysed, some 23 measurements and 18 meristics were recorded and complemented with several qualitative observations. Multivariate techniques used were primarily Principal Component Analyses (PCA). Non-parametric, distribution-free tests such as the Mann-Whitney U test were used for univariate comparison. Early in the project a priority list of groups for special study was agreed among project partners. These focused on economically and ecologically important species, particularly *Lethrinops*, *Mylochromis anaphyrmus*, *Copidochromis virginalis* complex and *Placidochromis* sp. 'platyrhynchus'

Lethrinops complex

The deep-water *Lethrinops* species-complex was the first group specifically studied by the project. It is one of the major groups targeted by deep-water fisheries and the taxonomy is very complex. The work was well complemented by an ongoing study at the start of the project on the shallow-water *Lethrinops* (Ngatunga & Snoeks, 1999; Ngatunga, 2000). The deep-water taxa examined were the *L. longimanus-macracanthus-mylodon* group, the *L. gossei*-complex and the *L. longipinnis*-complex. Based on re-identifications of the collections at Senga Bay, distribution maps were plotted for all taxa examined. The species of the *L. longimanus-macracanthus-mylodon* group were readily separated. In contrast, the existence of two subspecies within *L. mylodon* could not be confirmed owing to the lack of specimens from the type locality of *L. mylodon borealis*. In contrast geographic variation was found for *L. longimanus* between the populations from the north and northwest compared with those from the south and south-eastern parts of the lake. These observations need further elaboration to find out whether *L. longimanus* as currently defined is polyspecific. Of the deep water fish, *Lethrinops* sp. 'deep-water albus' is morphologically closer to *L. longipinnis* than to *L. albus*. Within what is regarded as *L. longipinnis*, we could detect four different species, based on a thorough multivariate analysis. Despite significant progress with unravelling the taxonomy of *Lethrinops* further work is required, especially on the generic relationships between the shallow-water and deep-water *Lethrinops* and *Placidochromis*.

Genetic supporting work done by UHULL.DBS.FG found no evidence for substantial genetic differences between samples of *P. platyrhynchus*, although some small but significant differences between samples suggest that gene flow (i.e migration) between areas is not extensive. In contrast, significant differences were observed among the samples of *Lethrinops* sp. 'deep-water albus', both within and between geographically distinct shelf areas, with by far the most distinct samples coming from the area near Nkhotakota. The results for *L.* sp. 'deep-water albus' are consistent with

restricted migration between areas and/or the presence of cryptic taxa (species). Work on species molecular systematics using 592 base pair DNA sequences from 50 individuals assigned to 18 species of *Lethrinops* and *Taeniolethrinops* were aligned and analysed for phylogenetic relationships. As found by several recent studies of lake Malawi cichlids, genetic divergence between species of these genera is not great enough to allow unambiguous associations within and between species to be discerned. However, a major division between two groups of species, one containing all *Taeniolethrinops* species studied plus *L.albus*, *L.marginatus*, *L.auritus* and *L.cf fucifer*, the other containing all other *Lethrinops* species studied, was identified. Inclusion of these species within a tree of the wider Lake Malawi haplochromine flock indicates that the first group lies within the so-called “non-mbuna” or “demersal” clade, and that the second group lies within the so-called “mbuna” clade. No statistically supported associations could be identified between species within the groups, or confirmation of individuals to their putative species.

Mylochromis anaphyrmus

The third important study of this task was that on the geographical variation in populations of *M. anaphyrmus*, chosen for this study as a representative of the shallow water demersal community. Small but significant morphological differences were found among all *M. anaphyrmus* populations examined. These results confirm the results of genetic work (Duponchelle, et al. 2000) showing restricted gene flow among these populations. Populations in this species are, therefore, most likely not part of a large uniform ‘stock’ but are separated by restricted gene flow and likely to have some degree of independent dynamics.

Copadichromis virginalis complex

Copadichromis virginalis has provided some difficulty for taxonomists but it is a common fish, found by Turner (1996) as one of the most abundant taxon in his 1992 survey, comprising almost 4% of the total sample weight. It often dominates catches, on occasion comprising 86% of the sample weight. **IRSNB.FBL** aimed to study the geographic variation in *C. ilesei* (which was considered identical with the *C. sp.* ‘virginalis kajose’ form), as a complement to other work (Taylor & Verheyen, 2001) done during the project on the population substructuring based on microsatellite data. However, taxonomic problems were found when comparing the *C. ilesei* types with the ‘kajose’ types. Therefore, first, a more elaborate study was started involving the three species in the *C. virginalis* complex (*C. virginalis*, *C. sp.* ‘virginalis kajose’ and *C. ilesei*) and, subsequently, the geographic variability in *C. sp.* ‘virginalis kajose’ was analysed.

The project found three distinct species within the *C. virginalis* complex. *Copadichromis ilesei*, which was believed to be conspecific with the ‘kajose’ types of *C. virginalis* (Konings, 1999) appeared to be distinct. Pending its formal description, the ‘kajose’ form of *C. virginalis* should therefore be referred to as *C. sp.* ‘virginalis kajose’. *Copadichromis virginalis* can be distinguished with relative ease from the other two species by its deeper body and smaller size at maturity. The two elongate species, which are of similar body shape and size at maturity can be distinguished on the basis of other characters. There appear to be ecological differences as well. *Copadichromis virginalis* and *C. sp.* ‘virginalis kajose’ are demersal sand-dwelling species, and are mostly collected by bottom trawling, up to great depths. *Copadichromis ilesei* has been reported to be associated with rocks. and has been

collected at very shallow depths (Konings, 1999). Based on a population-level study on microsatellite DNA analyses *C. sp. 'virginalis kajose'* does not comprise one single lake-wide population, but is divided into smaller subpopulations that exchange relatively few migrants. The morphometric results demonstrate that this population substructuring is also found within the species' morphology.

IRSNB.FBL collected 280 *Copadichromis* sp. 'virginalis kajose' from demersal trawl samples taken on Lake Malawi in 1998 and 1999. Additional samples were donated by the SADC/GEF Biodiversity Project. All samples were trawled at between 50 and 75 metres depth over an area of approximately 1500 metres length, with a minimum of 45 and a maximum of 72 individuals per population. Total DNA was extracted from ethanol preserved fin clips using Proteinase K digestion and salt precipitation, following a protocol modified from Aljanabi & Martinez (1997). Extracted DNA was resuspended in 200µl of autoclaved Milli Q H₂O. Microsatellite DNA markers reveal small but significant levels of population substructuring over all populations ($F_{ST}=0.004$, $P=0.002$; $R_{ST}=0.019$, $P<0.00001$). This structuring was low and over a much larger geographic scale when compared with previously published studies of the mbuna (rock-dwelling species), but greater than that found in pelagic cichlid species inhabiting Lake Malawi. The study suggests that there is low but significant levels of genetic substructuring in this demersal species.

Deep-water *Placidochromis*

During the SADC/GEF Biodiversity Project, a new sub-flock of deep-water dwelling, closely related, small to medium-sized cichlids was discovered, which are tentatively placed in the genus *Placidochromis*. (Hanssens, 1999a; Snoeks, 2001). A first extensive report on these taxa appeared in the final report of the SADC/GEF project (Hanssens, 1999b). During the current project, work on this group, extended by **MRAC.LI**, resulted in the description of 47 species, which makes it one of the most diverse species assemblages in the lake. A dedicated chapter on these fishes will be included in a book to be published soon (Snoeks, in prep).

UMW.DB investigated the genetic distribution of commercially exploited cichlids of the inshore artisanal fisheries of the lake. This information complemented the species identification using morphometrics, which was carried out by other partners working on the task 4. The work was based mainly on microsatellite DNA analysis using an ABI Prism 310 Genetic Analyser. To accomplish this, work was done under a title, "Zoogeographical Distribution and Population Structure of *Taeniolethrinops praeorbitalis* exploited by Artisanal Fishermen in the Inshores of Lake Malawi". A 1998 survey identified suitable sampling sites for *T. praeorbitalis* in Nkhota-kota, Salima and Mangochi districts where the species was landed from, mainly, gillnets and seine nets. In 1999 *T. praeorbitalis* specimen were collected from fish landing docks in Nkhota-kota District, in the central region, and Mangochi district, in the southern region. Tissues of about 5-10 mm² were extracted using scalpels from each fish and preserved in 95% ethanol in vials, which were properly labelled. Later the specimen were stored at <4 °C.

A summary of number of alleles showed that all the populations exhibited relatively high allelic diversity, with no significant difference in allelic diversity between Mangochi and Nkhota-kota populations. A summary of Hardy-Weinberg Equilibrium (HWE) tests indicated that at six loci almost all population showed significant

departure from HWE. A low and insignificant positive correlation between genetic and geographical distance ($Z = 0.06$, $P = 0.65$) concurred with MDS analysis results, which showed genetic relationships not corresponding with geographical distance. Overall, among the Mangochi and Nkhota-kota populations, there is still considerable amount of local genetic diversity, indicated by a good proportion of rare alleles represented by margins between observed and effective number of alleles. Although the Mangochi populations generally experience a higher exploitation pressure, their allelic diversity was not significantly different from that of Nkhota-kota populations.

Problems encountered

Although no real problems were encountered with the execution of the fish taxonomy work, it is clear that the difficulties of Malawi cichlid taxonomy is even greater than anticipated. An obvious case in point is the discovery of more than 40 new species in the sub-flock of the deep-water *Placidochromis*. Clearly as only just over 300 of the estimated 800 or more species are scientifically described, there is still a long way to go for a full taxonomic record. Even on a higher level, taxonomic problems are acute. Many problems on the genus level persist, or emerge, as new taxa are discovered that do not seem to fit the current genus definitions. During this project population level characteristics using morphometric techniques were examined for the first time. This resulted in a clear indication that non-mbuna species are not homogeneous in their morphology over their distribution range.

Task 5. Fishery assessment and growth rates of demersal fish. Lead partners: USOU.DBE and MNRMW.FD.FRL. Other partners: TANZ.FRI

Activities and results

Despite challenging logistical problems, the project made significant progress with a programme of artisanal data collection in Tanzania and Mozambique in collaboration with the SADC/GEF Biodiversity Project and the University of Waterloo, Canada. The demonstration of the feasibility of this is important, as the artisanal fishery represents the most intense impact on fish stocks in the lake. Considerable progress was made in synthesising artisanal fish catch sampling data from Malawi. Artisanal fishery yields have been approximately stable for the last 15 years and, lake-wide, the Malawian artisanal fishery continues to be largely dependent on small low-value zooplankton-feeding cichlids (Utaka) and cyprinids (Usipa). Yields of the higher value catfish and tilapias (Chambo) have declined, and now comprise less than 20% of the total catch. The river spawning cyprinids (ntchila etc) are presently of very low importance probably as a result of high targetted fishing effort, but also disturbance of the river catchments by agriculture. **USOU.DBE** and **MNRMW.FD.FRL** in collaboration with the GTZ-funded NARMAP programme, developed a catch-sampling programme that recorded catches to species level, thereby enabling the breakdown of national statistics collected by aggregate marketing categories into their likely biological species composition. These were then be re-aggregated for the modelling studies, according to the functional groups identified through analysis of trophic guilds and other assembly rules drawn from community ecological studies.

Fisheries catch-effort and species-composition data were also obtained from a one-year sampling programmes in Metangula, Mozambique and, by **TANZ.FRI**, along the Tanzanian coast. These fisheries were largely dependent on mid-water feeding species, such as the small cyprinid *Engraulicypris sardella*, zooplankton-feeding

inshore cichlids (*Copadichromis spp.*) and the pelagic cichlids (*Rhamphochromis* and *Diplotaxodon*). River-spawning species, especially cyprinids, were more important than on the more densely populated Malawian coasts, probably owing to lower fishing effort and lesser disturbance of the Mozambican and Tanzanian river catchments. Demersal species were far less important than in the southern Malawian shelf areas.

Appraisal of artisanal fisheries stock assessment methods:

Fishery management requires a design for maximum sustained yield (economic or biomass). It is now recognised that in most of the world's managed fisheries this has not been achieved. In less developed countries, particular problems arise when the management approaches recommended are too 'data hungry' and consequently expensive to implement (Mahon, 1997). The adoption of inappropriate monitoring strategies can lead to a serious imbalance such that extensive data are collected but no funds are left to analyse them and, most significantly, act on the advice generated. The fisheries of Lake Malawi, although important (est. 35-40 000 t annual yield), have to be managed on a limited economic base. The fishery in Malawi is largely of a small-scale non-mechanised nature with a mechanised trawl fishery operating in the southern part of the lake. The fishery mainly employs paddle-powered dugout canoes, fishing gill and seine nets, handlines and longlines, and basket and fence traps. Recent records estimate the total yield from the small-scale fishery to have fluctuated around 30,000 tons over the last ten years. The total catch of trawl and ringnet fisheries has been around 4-5,000 tons per annum. Some of the key fish stocks are declining, fish community compositions are changing and fishing effort is rising rapidly. This situation, combined with the time lag in data analysis and the lack of enforcement, leaves the fisheries in a highly vulnerable state. An effective assessment and management strategy is needed urgently.

In 1976, on the advice of FAO, the Department of Fisheries opted for a 'Stock Assessment Driven' (SAD) approach to fisheries management and a long-term programme of routine catch monitoring was initiated. Monitoring of trawl fisheries requires catch and effort records to be submitted to the Department of Fisheries on a monthly basis. The submission of these records is a condition of the granting of the license to fish. The small-scale fisheries are monitored through the combination of a boat-based 'Catch Assessment System' (CAS) introduced in 1976, and a gear-based system - the 'Malawi Traditional Fisheries' system (MTF) introduced to the Mangochi District in 1990 by FAO. Total fishing effort is assessed through annual Frame surveys at all landing sites throughout the Malawi sector of the lake. Survey results are used to estimate total monthly landings and fishing effort for all traditional fisheries along the lake.

MNRMW.FD.FRL research found that most fishing gears in the artisanal fisheries on the lake are illegal because they do not have the legally prescribed mesh size. There has been a shift in mesh sizes from large to small meshes for most gears, which in most cases is caused by decline of large fish in the fisheries. The small mesh gears pose a threat to biodiversity because of the high species diversity in the catch composition. They also catch small immature fish of large species and both growth and recruitment overfishing are imminent with high fishing pressure caused by increasing effort as depicted from the Frame Survey data. Localised overfishing is becoming a common phenomenon in the traditional fisheries of Lake Malawi. The

shift in mesh sizes of the gears has also been accompanied by modifications of gears and fishing techniques, which are also ascribed to the declining of the large fishes.

The legal prescribed mesh size for trawler nets is 38 mm and the review based on the trawl selectivity studies indicate that the 38 mm mesh sizes clog within 15 minutes and yet the average minimum trawling duration is about 120 minutes. Most of the fish caught are also immature. In practise therefore the trawl fishery has no mesh size regulations and also pose a threat to biodiversity.

The presence of some deep-water species in the artisanal gears is manifest that the fishery is tapping the offshore deep fish resources. The current experience from experimental trawl fishing supports this. Trawling on the north eastern side of the southeast arm is not easy currently because of the numerous illegal day setting gillnets from 40 to 80 m water deep. The owners of these gears guard them, making trawling in the midst of fishers almost impossible. Open water seines exploit fish in waters < 40 m deep while gillnets are set in waters of > 40 m deep probably to avoid social conflicts. This fishing pattern entails that bottom trawling is confined to waters greater than > 80 m.

The integration of the findings strongly indicates that the southeast arm where most of the work was based is under severe fishing pressure that requires sustainable management strategies to be placed immediately to minimise further environmental deterioration. Virtually all the depth ranges seem to be exploited at present as vindicated by these research activities. There is a proliferation of small meshed gear fisheries in the area, which is extremely destructive to the fisheries resources and the mode of their operations also accelerates environmental degradation.

In view of the rapid change in gear pattern utilisation, general increase in fishing effort, the fast decline of economical value species with no signs of rebuilding and the absence of effective management strategies, the Government priority area should be the conduction regular monitoring surveys to address the changes taking place in the fishery. The selectivity research activities can be considered as complementary monitoring surveys of the artisanal fisheries, which have often been neglected due to the complex nature of the fisheries. The artisanal fisheries have been monitored through Catch and Effort Surveys which has short falls in terms of accuracy and the fact that the analysis of the data lags behind, because of some administrative logistic problems in the collection of the data from various districts. CAS tends to provide meaningful results if it is up to date and does not show the biological impact of fishing on the fish stocks. It is therefore recommended that the long-term research studies established through the EU initiative should continue to be part of the monitoring programme for the artisanal fisheries. The studies will give information on the changes taking place in different fisheries thereby providing useful input in the formulation of the management strategies of the lake. Due to financial resources constraints, bi-annual traditional selectivity studies are recommended on a regular basis.

Stock management advice has, until recently, been based upon an analysis of time series of CPUE data to determine maximum sustainable yields through use of surplus production models. Subsequent management recommendations have been based largely on technical restrictions on fishing gears and restrictions on fishing areas or

times, and minimum size of first capture. In recognition of the shortcomings of surplus production models, the Department of Fisheries has recently recommended adopting a 'precautionary approach' where a level of CPUE is selected below which catch rates should not be allowed to drop. The threshold level of CPUE has been called $CPUE_{pa}$, calculated as 45% of $CPUE_{max}$ which, in the absence of stock estimates for virgin biomass, is the mean CPUE over a period of five to ten years of relatively high CPUE. Effective management of the fisheries has, however, been extremely limited owing to a lack of finance and manpower for enforcement of policies and much of the catch and effort data unprocessed. The backlog in data analysis has limited reporting and by 1999 the analysis of time series for CPUE was three years in arrears. Any decline in catch rates would be unlikely to be detected in time for management action. The failures of current management appear to have arisen partly through an imbalance in the allocation of resources to data collection compared with analysis and enforcement. A more structured approach to stock-assessment based management system is required.

The combined Lake Malawi fisheries exploit in excess of 300 species, which exhibit a broad range of life history traits that may respond differently to fishing pressure. A single species management approach and use of single species fisheries models are inappropriate. Management strategies based on a more holistic approach are required, but many of the multi-species, multi-gear and ecosystem approaches are likely to prove too costly. The choice of management strategy is, therefore, not obvious. We suggest, however, that:

1. Management objectives must be clarified;
2. The level of available management resources (human and economic) must be determined;
3. Potential options for management strategies and their data requirements and costs should be determined; and
4. A management strategy should be chosen which can meet the management objectives while remaining within the limits of the economic and human resources available for its implementation.

Malawi fishery objectives are to maximise the sustainable yield from fish stocks, improve efficiency of exploitation, processing and marketing and exploit all opportunities to expand existing, and develop new aquatic resources, while taking care to protect species biological diversity. There has been much less explicit consideration of fisheries policy with respect to issues of employment, equity and resource allocation within the catching sector. It remains unclear whether management policy favours a drive towards economic gains or high protein yields. Although biological diversity within the lake is highly valued internationally and fisheries sector policy does state the intention to conserve biodiversity, the higher priority of the country will be to feed its people and generate income from natural resource exploitation; as testified by recent (Jan 2003) African Development Funding of \$10.5 million dollars to increase utilization of fisheries resources in five Lake Malawi districts, following regional food shortages. Preservation of biodiversity needs to be considered within an integrated strategy of maintenance of productivity of the fisheries.

The current stock assessment based management approach could be significantly improved through a major cut back in the scale of data collection and a lake-wide switch to the entering of data directly onto computers, rather than requiring a great deal of transcription and manual calculation. Attention needs to be directed towards an appraisal of the precision of fleet size estimates derived from the frame surveys, possibly through repeated re-sampling on a small area. These actions should help to reduce errors in data collection and free up personnel and financial resources to ensure timely analysis of the data and the implementation and enforcement of management recommendations. Consideration should be given to the inclusion of locally based fisherfolk in the catch monitoring programme, as the project has piloted in Tanzania and Mozambique.

Research trawling

Research trawling to assess biomass and species composition of demersal fish was completed in January 2000. Three lake-wide trawl surveys and three more localised surveys were conducted using the RV Usipa. This data was supplemented by analysis of trawl data held at the Monkey Bay Fisheries Research Unit. Analysis of mean catch rates for all sites indicates that although high catches were made in individual tows in the central and northern lake, catches in the heavily exploited southern part of the Lake were not significantly lower. This may be owing to the higher natural productivity of these areas. There was no consistent trend with bottom depth.

An analysis of historical data, using modern multivariate techniques, demonstrated that trawl catches are becoming more similar (mean similarity 38.89 in 1973 and 54.28 in 1998 - Bray-Curtis similarity index). K-dominance curves show that the community has become dominated (in terms of biomass) by fewer species in recent years. There was no significant reduction in species richness over time, at the restricted taxonomic level used in the analyses. The trend for increasing dominance was, however, reversed during the last survey period (1995-98). While this may indicate a degree of community resilience to fishing, detailed analysis of species composition indicated that populations of several 'key indicator' species had not only failed to recover since the early 1990s, but in some cases there was evidence of further declines. These species appear to be persisting in areas where trawling is presently light or absent, and to have disappeared from heavily trawled areas. This makes it highly probable that expansion of trawling in the northern areas of Lake Malawi will lead to the extermination of these species.

The fisheries of Lake Malawi are multi-species as indicated by the selectivity studies which confirm that single species models that have been employed in the management of the demersal fisheries are inappropriate, which allow the exploitation of one fish stock at the expense of the other. Management strategies based on the holistic approach may provide effective management of the fisheries resources on the lake.

The studies show that most fishing gears in the artisanal fisheries on the lake are illegal because they do not have the legally prescribed mesh size. There has been a shift in mesh sizes from large to small meshes for most gears, which in most cases is caused by decline of large fish in the fisheries. The small mesh gears pose a threat to biodiversity because of the high species diversity in the catch composition. They also catch small immature fish of large species and both growth and recruitment overfishing are imminent with high fishing pressure caused by increasing effort as

depicted from the Frame Survey data. Localised overfishing is becoming a common phenomenon in the traditional fisheries of Lake Malawi. The shift in mesh sizes of the gears has also been accompanied by modifications of gears and fishing techniques, which are also ascribed to the declining of the large fishes.

The legal prescribed mesh size for trawler nets is 38 mm and the review based on the trawl selectivity studies indicate that the 38 mm mesh sizes clog within 15 minutes and yet the average minimum trawling duration is about 120 minutes. Most of the fish caught are also immature. In practise therefore the trawl fishery has no mesh size regulations and also pose a threat to biodiversity.

The presence of some deep-water species in the artisanal gears is manifest that the fishery is tapping the offshore deep fish resources. The current experience from experimental trawl fishing supports this. Trawling on the north eastern side of the southeast arm is not easy currently because of the numerous illegal day setting gillnets from 40 to 80 m water deep. The owners of these gears guard them, making trawling in the midst of fishers almost impossible. Open water seines exploit fish in waters < 40 m deep while gillnets are set in waters of > 40 m deep probably to avoid social conflicts. This fishing pattern entails that bottom trawling is confined to waters greater than > 80 m.

The integration of the findings strongly indicates that the southeast arm where most of the work was based is under severe fishing pressure that requires sustainable management strategies to be placed immediately to minimise further environmental deterioration. Virtually all the depth ranges seem to be exploited at present as vindicated by these research activities. There is a proliferation of small meshed gear fisheries in the area, which is extremely destructive to the fisheries resources and the mode of their operations also accelerates environmental degradation.

In view of the rapid change in gear pattern utilisation, general increase in fishing effort, the fast decline of economical value species with no signs of rebuilding and the absence of effective management strategies, the Government priority area should be the conduction regular monitoring surveys to address the changes taking place in the fishery. The selectivity research activities can be considered as complementary monitoring surveys of the artisanal fisheries, which have often been neglected due to the complex nature of the fisheries. The artisanal fisheries have been monitored through Catch and Effort Surveys which has short falls in terms of accuracy and the fact that the analysis of the data lags behind, because of some administrative logistic problems in the collection of the data from various districts. CAS tends to provide meaningful results if it is up to date and does not show the biological impact of fishing on the fish stocks. It is therefore recommended that the long-term research studies established through the EU initiative should continue to be part of the monitoring programme for the artisanal fisheries. The studies will give information on the changes taking place in different fisheries thereby providing useful input in the formulation of the management strategies of the lake. Due to financial resources constraints, bi-annual traditional selectivity studies are recommended on a regular basis.

Problems encountered

Estimates of demersal species composition were limited by the number of lake-wide research cruises and one cruise had to be abandoned because the trawl net was damaged on a sunken tree while fishing the uncharted waters off Mozambique. However, access to data collected by the FRU and SADC/GEF projects largely compensated for these problems. We did not collect data on seasonal changes in fish communities, fish diets, reproduction and growth because we were aware that this was concurrently being carried out by the SADC/GEF project.

Task 6. Fish diet analysis. Lead partner: UEA.ODG. Other partners MNRMW.FD.FRL and UDTC.DZ.

Activities and results

Extensive diet analysis of the main components of the demersal fish stock was done by **UEA.ODG** and **MNRMW.FD.FRL**, with taxonomic support from **UDTC.DZ**. Work was focused particularly on species of potential importance for energy flow in the demersal community with elucidation of percentage composition of food items in the diets of 109 fish species. These data were used to define ‘trohic guilds’ – collections of species using similar and distinctive combinations of food categories. Hierarchical agglomerative clustering and ordination methods were used to identify groups of species with common diets. Ten trohic guilds were identified and fractional trohic levels calculated for all 109 species, based on the methods of Pauly et al (2000). Use of Multi-dimensional scaling (MDS) plots demonstrated clearly that guild composition is more highly conserved than species composition for those sites which were previously identified within Task 4 as most dissimilar in terms of species compositions. As species differentiation between sample areas has not led to significant parallel changes in trohic guild compositions it is concluded that the species replacements are trohic equivalents. We estimate that at least 40% of species within the Lake Malawi demersal fish community are trohic analogues.

Food consumption rates were calculated by fitting consumption-evacuation rate models to data collected from diel sampling of stomach contents for the dominant species, following the methods outlined in Allison et al., (1996) and this information fed into the trohic modelling work of Task 8. A number of species representing dominant examples across a range of trohic guilds were targeted for this work. Samples were collected from both the *shallow* (30 m depth) and *deep* (125 m) demersal. Main shallow taxa targeted were *Mylochromis anaphyrmus* (molluscivore), *Oreochromis* spp. (detritivore), *Nyassachromis argyrosoma* (zooplanktivore), *Copadichromis quadrimaculatus* (zooplanktivore), *Lethrinops longipinnis* (generalist omnivore) and *Alticorpus geoffreyi* (benthivore). Deep water targeted taxa were *Lethrinops gossei* (feeder on chironomids and *C.edilus*), *Lethrinops oliveri* (detritivore), *Placidochromis platyrhynchus* (feeder on shrimps), *Diplotaxodon macrops* (zooplanktivore), *Lethrinops altus* (omnivore on invertebrates) and *Aulonocara minutus* (generalist omnivore).

Calculating food consumption rates from diel stomach contents analysis is, however, difficult and time consuming as there is a need to many samples across a diel cycle, and with sufficient replication across a range of size-classes in order to derive reliable estimates of food consumption rates. Most studies rely extensively on use of empirical models linking fish morphometry to consumption/biomass ratios

(Palomares and Pauly, 1998). Food consumption rates were, therefore, also calculated for an additional 35 species using the empirical method. Outputs from Task 6 were important inputs to the trophic modeling of Task 8.

Problems encountered

In situ calculations of fish consumption rates are difficult and depend on collection of sufficient numbers of fish across a range of size classes. In addition, a variable proportion of fish stomach contents are lost due to the pressure change on being brought to the surface from depth. Attempts to select individuals that had retained their stomach contents may not have been wholly successful with partial evacuation being a possibility. This can lead to low estimation of Q/B values (see Task 8). Further difficulties with these estimates pertain to piscivores, which rely on the occasional consumption of a few large prey items. While these difficulties need to be taken into account in the interpretation of results, overall the fish diet analysis and consumption rate estimates are considered to provide sufficiently robust data to determine trophic structure of the demersal fish community, which was also supported with stable isotope analysis of Task 7, and to provide meaningful input to the trophic modeling of Task 8.

Task 7 Stable isotope analysis. Lead partner: UEA.ODG

The accuracy of trophic analysis based on stomach-contents data was tested by **UEA.ODG** using stable isotope analysis. The trophic levels calculated from $\delta^{15}\text{N}$ values were compared with those obtained for the same 34 species using dietary analyses. A Sign test of the difference between estimates from the two methods found no significant difference ($z = -1.281$; $p > 0.05$). On the basis of these findings it is concluded that dietary data from stomach analyses provide a fair representation of the long-term diet compositions of the species examined.

Problems encountered

The Stable Isotope sub-contract between **UEA. ODG** and colleagues in the School of Environmental Sciences was based on an informal trust relationship – we would be able to obtain more samples than we had budgeted for, in return for sharing the authorship of the results. Unfortunately, this informal agreement did not work in practice, and many of the samples collected remain unanalysed. As there was no formal contract between ourselves and ENV UEA regarding the minimum number of samples to be processed, we cannot legally enforce the completion of the work. Nevertheless, the work done has generated sufficient results to fulfil its original purpose as a means of validating other methods of examining trophic structure. **UEA.ODG** and **UDTC.DZ** are seeking supplementary funding to complete analysis of the remaining samples.

Task 8 Trophic modeling. Lead partner: UEA. ODG. Other partners: All.

Two Ecopath models have previously been developed for the pelagic zone of Lake Malawi (Degnbol 1993; Allison *et al.* 1995) but, until now there has been no complementary study of biomass flows through the demersal community. One of the main conclusions of the first pelagic model by Degnbol (1993) was that "the pelagic ecosystem of central Lake Malawi produces midge larvae and midges (*Chaoborus edulis*), not fish.". However, the second model (Allison *et al.* 1995) demonstrated that "...*C. edulis* is clearly more important to the fish community than had previously been supposed..." with an estimated 50% of production being consumed by pelagic

fish predators. They also suggested that many demersal fish species might be feeding on *C. edulis* larvae that migrate into the sediments on a diel cycle to seek refuge from pelagic predators. As *C. edulis* is a pelagic feeder (Irvine 1997) it was therefore concluded that "...the community of demersal fish is directly tied to pelagic productivity, rather than indirectly through a detrital food chain." (Allison et al., 1996b). These results provided a main stimulus to present study. Without further information on the demersal food web structure and dynamics the role of *C. edulis*, the nature of the proposed benthic-pelagic coupling, and the relative importance of pathways supporting the demersal community remained unknown.

Using outputs from tasks 5, 6 and 7 system modeling was done by **UEA.ODG** using *ECOPATH* model and ECOSIM scenarios (Walters, 1997) to describe trophic structure of the demersal zone and estimate impacts of changing fishing practices on the fishery. The generalised food web spans four trophic levels and has two main bases in detritivory and planktivory. The consumption of detritus is largely by benthic invertebrates although a few fish groups, notably *Oreochromis* spp., specialise in sifting diatoms and other organic matter from the detrital ooze. At trophic level 3 a number of fish groups feed on the benthic invertebrates. Zooplankton is imported into energy flow through the fish community at trophic levels 3 to 4 through predation on carnivorous and herbivorous copepods and *C. edulis* larvae. Most fish species are then subject to predation by a large number of piscivorous fish species. The apex predators are *Bagrus meridionalis*, the clariids and some of the large cichlid piscivores that suffer little predation themselves. The only source of primary production within the demersal system itself is macrophytes and algae that are restricted to the shallow water demersal. The longest potential food chain, with six levels, passes from diatoms, through herbivorous copepods, carnivorous copepods, *C. edulis* larvae, fish zooplanktivores, cichlid piscivores, to an apex predator such as *Bagrus meridionalis*.

The euphotic zone of the lake, which extends to approximately 50 m, supports photosynthetic activity for the production of the phytoplankton and algae that form the basis of the pelagic and inshore demersal food webs. Organisms living within the euphotic zone can directly exploit these primary producers but those organisms living in deeper water such as in the offshore demersal community will have to rely on the transfer of organic material from the pelagic to the benthic system. The three main transfer mechanism are: through waste products and dead organisms sinking into the demersal habitat; through demersal species migrating into the pelagic to feed; and active migration of pelagic species into the demersal habitat where they are consumed by demersal predators.

Estimates of relative importance of the different pathways of benthic-pelagic coupling to demersal fish production suggest that only 2.5% of the biomass consumed at the lowest point of entry into the demersal system is of demersal origin comprising a combination of flows to detritus from fish demersal fish groups and primary production by macrophytes and algae. A "detrital rain" of dying pelagic organisms and faeces accounts for a further 6 % of biomass import. A further 4% of demersal fish biomass is imported as *C. edulis* larvae that are consumed on their migration into or from the sediments. The greatest flow of biomass into the demersal fish is, however, through consumption of copepods (55.5%) and diatoms (33%) from the pelagic ecosystem. Diatoms are most likely consumed from within the sediments having dropped out of the pelagic.

In summary, the demersal system appears to rely most heavily on biomass imported from the pelagic through consumption of copepods by fish migrating vertically to feed in the pelagic, and through a fall out of diatoms which are consumed by fish sifting them from the sediment ooze. Estimated transfer efficiencies between Lake Malawi trophic levels were found by the current work to be highest between levels II and III, where they reach 23%. This value far exceeds the 10% general rule for biomass transfer efficiencies between trophic levels (Slobodkin 1960) and points to highly efficient use of food resources by the primary consumers in Lake Malawi. Efficient energy transfer would be expected in ancient lakes with evolution of large numbers of species.

Scenario modelling by **UEA.ODG** indicated that persistence of current fishing levels will lead to trophic, as well as species change. An initial simulation, based on maintaining 1999 levels of fishing effort for the whole lake ecosystem, was run for a 20 year period to provide the benchmark against which to evaluate simulations for alternative fishing regimes. Simulations were then run to predict the impact of an overall doubling of fishing yield across all gears. Under current fishing pressures clariids and “Detritus and diatom Feeders” were predicted to decline and reach a stable state after about 15 years. The total catch from the combined fisheries was predicted to remain relatively constant. An overall doubling of fishing pressure across all gears predicted a decline in biomass of an additional six groups, three of which - *Bagrus meridionalis*, clariids and the detritus and diatom feeding fishes - were predicted to be lost from the system. Ecosim, used to predict the fishing pressure increase that gives the greatest total yield, indicated that a five times increase in fishing effort would provide the greatest total yield, with a simplification of the community through the loss six fish groups including *Bagrus meridionalis*, Clariids, Chironomid feeders, *Syndontis njassae*, Detritus & benthic invert feeders and *Chaoborus* feeders. This assumes that the main catch will then be dependent on Molluscivores, Caridina feeders, and Oligochaete feeders. The change in trophic pathway implied is, however, unlikely to occur in practice and it is more probably that the productive basis of the ecosystem would collapse before that occurred.

In summary, increasing fishing (as is likely under the current pressure on stocks and the lack of enforcement capacity) will cause change in both species composition and trophic structure, although total fish yields may continue to increase, particularly if fishing is expanded into areas where there is currently a low level of fishing effort (the deep water demersal and offshore pelagic zones). Changes in trophic structure as a result of such increases, and irrespective of the effects on ecosystem buffering as discussed above, may lead to other unpredictable outcomes. Currently, the mean trophic level of harvested fish is 2.99 and shows the fisheries to be harvesting from relatively high in the food-web. It has been demonstrated on a global scale that fisheries tend to fish down the food-web as demand outweighs supply for existing fisheries (Pauly *et al.* 1998). There are consequent dangers of a management strategy which allows for fishing down food webs when, in contrast to the continued increase in catch that may be expected when fishing down food webs, there may instead be abrupt phase shifts showing marked reductions or stagnation of catches. One possible explanation given is that the fisheries may have induced changes in food webs through trophic cascades (Carpenter *et al.*, 1985). Tracking the mean trophic

level of the fishery over time may provide a useful warning indicator of potential ecosystem overfishing.

Technology Implementation Plan

This is submitted as a separate outcome of the project. In general, the project results have provided a number of recommendations for future management, research and monitoring relevant to the sustainable use of the demersal fishery of the lake. These are:

1. The management objectives for the lake should be clarified and, preferably, agreed among the riparian states;
2. Management strategy should be chosen which can meet the management objectives while remaining within the limits of the economic and human resources available for its implementation;
3. A more structured approach to the monitoring of the fisheries and a stock-assessment based management system to include all important stakeholders in the Malawian waters;
4. Further basic monitoring systems should be supported for the artisanal fisheries along the coastline of Tanzania and Mozambique.
5. Further work is required to quantify the production base of the fishery, including the role of microbial communities;
6. Continuation of high-quality taxonomic and ecological work should be encouraged in order, at least, to further catalogue the fish communities and their role in trophic pathways;
7. Monitoring of demersal catches should include assessment of trophic categories of landed fish in order to track potential shifts in trophic structure of the demersal fish community;
8. The multispecies fisheries should be managed to retain diversity as a safeguard against collapse of stocks.

The project has no plans directly exploit or patent the results of the project, although the knowledge gained is of direct use for the future monitoring and management of the fisheries.

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Conclusions

The results of the project have progressed the understanding of ecological structure and function of one of the world's most diverse ecosystems. It has provided information that is of direct relevance for the future protection of both the fisheries resource and biodiversity of the lake. The project provided novel findings on invertebrate community descriptions and distributions, measurements of bacterial production rates and distributions, and on fish taxonomy and distributions, and information on genetic integrity of stocks of some important demersal fish. The modelling work of the project linked the trophic compartments to provide the first estimates of energy flows through the demersal fish community and its link with that the pelagia.

Management recommendations arising for the project are summarized above under ***Technology Implementation Plan***. The implementation of lake management plans relate primarily to the Malawian waters, as it is in these that the most pressing issues occur. Recent shifts in community structure of fisheries and localized reduction in fish catches signal clearly the need for a greater understanding of impact from both commercial and artisanal fisheries. Recent food shortages in the region input of emergency donor funding (January 2003 African Development fund allocation of US\$10.5 million to enhance fisheries exploitation in five Malawian littoral regions (Likoma, Nkhata Bay, Nkhosakota, Salima and Mangochi)) highlight the expected importance that the lake has as a human food supply. Such efforts risk failure and even the accentuation of problems of overfishing, if not based on sound scientific information to support policies. Good ecological management supports economic strategies. The results of the project can very much be used towards the goal of sustainable fisheries management. In the coastal zone of Tanzania the project effected surveys of the artisanal fisheries. This provided the first attempt to provide basic information that can be used to help fisheries management. It is, however, only a first step as limited infrastructure and availability of trained personnel hinder further work. Institutional difficulties with reporting procedures provide additional obstacles to development of effective monitoring and management. In Mozambique the project, in conjunction with the Lake Malawi Biodiversity Project, instigated a pilot artisanal monitoring programme. As in Tanzania, the future development of scientific work is currently hindered by poor infrastructure and lack of trained personnel. In both countries the development of laboratories for fisheries science of the lake have not progressed as much as recent initiatives, particularly the SADC/GEF Lake Biodiversity Project would have hoped for.

Overall the EU funded project *The trophic ecology of the demersal fish community of lake Malawi/Niassa, Central Africa* can be considered a success story in that it accomplished its objectives and has supported the development of fisheries and ecosystem research and monitoring among scientists from EU and DC partners. There

are, however, also lessons learnt that relate mainly to issues of project management and the structure of this, and similar, projects. These are dealt with in the Management report.

Management Report

Organisation of the collaboration

The project commencement date was 1 March 1998 and the first six months was spent largely with the establishment of an infrastructure within Malawi. In August of that year the project established a base in Senga Bay Malawi, with the first research cruise in September 1998. The project was able to secure the loan of a vehicle from the British High Commission, Lilongwe, for the duration of time that EC partner scientists were based in Malawi. From the beginning, the project collaborated well with the SADC/GEF Lake Malawi/Nyasa Biodiversity Project until that project ended in July 1999. At that time one of the EU project scientists relocated to Monkey Bay, and was able to work closely with Malawi Fisheries, including use of an office within the Fisheries Institute, and with the project manager of the GTZ-funded *National Aquatic Resource Management Programme* (NARMAP). The relocation to Monkey Bay also ensured ready access to existing fishery data

The structure of the project comprised linkages among partners as outlined in the Technical Annex to the contract. The original proposal was set up in a way that allowed close links between EC and African partners. This scheme paired the following closely

Malawi Fisheries & TCD Dublin

Tanzania Fisheries & Southampton/UEA

Mozambique fisheries & Invertebrate studies of the Royal Belgium Institute of Natural Sciences

University Malawi & Genetic studies of the Royal Belgium Institute of Natural Sciences/University of Hull.

This provided an overlapping partnership of three important facets of the project: 1) Fisheries research; 2) Trophic dynamics; and 3) taxonomy and genetics. The project comprised six EU partners and three DC partners. The Government of Mozambique declined to participate late in the preparatory period but, nevertheless, was included as far as possible in planning and execution of the project.

One DC partner, UMW.DB, had a remit to focus on genetic variability of inshore fishes and collaborated throughout the project with genetic laboratories of IRSNB.FRL and UHULL.DBS.FG. The original format for the involvement of the Fisheries Research Institutes of Malawi and Tanzania was altered early in the project as it became apparent that 1) it would be difficult to employ a suitable qualified full time research officer and 2) suggestions by the Malawi Fisheries Unit (FRU) that a more effective project would occur if, rather than employ a temporary research officer, funding was assigned more directly to fisheries activities under the direct management of the FRU. Consequently a series of fisheries activities were agreed between the FRU and senior scientists of the project. These were designed in order to answer important questions related to gear selectivity, catch and gear surveys

within Malawi and catch efficiencies by a the R/V Ndunduma, one of a pair of research/commercial trawlers donated to Malawi by the Government of Iceland.

Alterations in project structure were agreed during the first year of the project that involved more effectively the existing fisheries research laboratories of Malawi and Tanzania at Monkey Bay and Kyela, respectively. This necessitated changes to the original scientific project structure but was done to provide a greater extent of research activity on the collection of fisheries data. The redirection of effort, while agreed among the project, nevertheless, placed more pressure on the capacity for analysis of fish diet and benthic samples.

Collaboration was generally satisfactory among all partners, although problems relating to financial mechanisms arose in the later part of the project (see below). Communications among EC partners and with UMW.DB were effective throughout the project. Communications with TANZ.FRI office at Kyela were sometimes difficult owing to poor infrastructure. Communications with Mozambique were variable. These difficulties were mitigated against in the early stage of the project by the support of the EC scientist Mr Darwall, based in Malawi. Operations in Mozambique were particularly challenging owing to poor infrastructure and safe methods for transfer of funds. An artisanal programme was, however, effected through collaboration with the SADC/GEF Lake Biodiversity project.

In the first six months of the contract the project purchased a variety of equipment, but also established the use of some additional items available for use for Dr Turner's previous research and the use of a UK DFID vehicle. At the conclusion of the period of fieldwork by EC partners, equipment purchased by the project was dispersed to the regional fisheries institutes at Kyela (Tanzania) and Monkey Bay (Malawi).

Meetings

The first project meeting, involving only EU partners was held in Southampton in February 1998 and just prior to the commencement date (Report of that meeting, see Annex II). At the start of the project the coordinator visited Malawi in March 1998 to establish the project. During that trip meetings were held with: Mr Mkoko and Bandula (Malawi Fisheries, Lilongwe), Dr Ambali (University of Malawi, Chancellor College, Zomba), Drs Ribbink, Bootsma, Snoeks and Mr Day, and Dr Taylor, visiting from Waterloo University, Canada (GEF/SADC Biodiversity project, Senga Bay), Mr Smit (Senga Bay), Mr Zgambo (Malawi Fisheries Department, Nkhata Bay), Mr Bulirani and Palsson (Malawi Fisheries Research Unit, Monkey Bay) & Dr. H. Potter (Dept. for International Development, UK, British High Commission, Lilongwe). Between 9th-23rd August 1998, Dr Turner of USOU.DB has meetings with staff at the headquarters of the Malawi Fisheries Dept in Lilongwe (Mkoko, Bandula, Helgasson), at the GEF project in Salima (Ribbink, Snoeks, Hanssens, Duponchelle, Ngatunga), the DANIDA bilharzia project at Cape Maclear (Bloch), and the Fisheries Research Station at Monkey Bay (Kachinjika, Bulirani, Palsson). In July 1998 the project coordinator met with Dr Martens in Brussels on 14 July to further discuss the project and interview an applicant for a post-doctoral position on the project.

In September 1998, while visiting Malawi for the first lake cruise the project coordinator discussed the project with: Malawi Fisheries HO staff D.D. Bandula

(Deputy Director), S. Mpila (new acting Director) and O. Kachinjika (Research Coordinator); A. Bulirani & M. Banda of the Fisheries Research Unit; Manuel Mazibe (Director of the Institute for Mozambique Fisheries Research), Claudia Tomas, Inocencio Elias Sotomane (Provincial Director of Agriculture and Fisheries for Niassa Province, Mozambique) and a number of Mozambican Research counterparts and students associated with the SADC/GEF programme; Prof. P. Bwathondi (Director General of Tanzanian Fisheries Research Institute), Mr Mlay, Director of the Kyela Research station, and Mr B. Ngatunga; C. Price (Fisheries advisor to DFID, UK); Dr R. Hecky (University of Manitoba, Canada's scientific advisor to SADC/GEF project; Dr. S. Guildford (University Waterloo, Canada). These meetings discussed project involvement of the partners (University of Malawi, Malawi Fisheries Department), collaboration (GEF/SADC Biodiversity project, University of Waterloo) and project logistics.

As part of the project coordinator's visit to Tanzania in conjunction with other work, meetings were held in Dar es Salaam, Tanzania, January 1999 with staff from TAFIRI (Prof Bwathondi; Director General), the Ministry of Natural Resources and Tourism (Mr Houle), and Mr Ngoli of the Tanzanian Cooperation for Scientific Research and Technology (COSHTECH). for two main purposes. These meetings included of the Ministry of Fisheries and of TAFIRI) and (COSHTECH). Despite a favourable initial reaction it was ruled that the project would need to pay for the permits (total cost US\$1850) prior to the cruise in March 1999.

The first overall project meeting, involving all partners and representatives from Mozambique was held in April 1999 in Malawi. The third project meeting, involving just EU partners was held in Brussels in November 1999. The fourth project meeting was held in Ireland in July 2000 and followed on from a successful international meeting on the *Great Lakes of the World*(GLOW II), organized by the project coordinator. Project personnel made five oral and two poster presentations at that meeting. At project meetings, progress, logistics of the project and the protocols for data inputs into the trophic models were discussed and agreed among partners. Minutes of the meetings are provided in Annex II of this report. A number of project partners met at the *Lake Malawi Management Symposium and workshop* held in Malawi in June 2001 and the 3rd GLOW meeting held in Arusha in February 2002. The project coordinator was represented by Will Darwall at the Management Symposium and met formally with MNRMW.FD.FRL and TANZ.FRI to discuss project progress. Attendance of project partners at GLOW III was insufficient to convene a project meeting.

In August 2002 the Project coordinator visited MNRMW.FD.FRL and TANZ.FRI in order to progress the delivery of the final reports and cost statements. This resulted in subsequent prompt submission of the information outstanding by MNRMW.FD.FRL, but final delivery from TANZ.FRI did not occur until early 2003. The reasons for this delay are unclear but appear to relate to administrative difficulties within the local and central offices of TANZ.FRI.

Exchanges

Two scientists from, respectively, UDTC.DZ and USOU.DBE were based in Malawi for about 18 months. On return to Europe these went to work at, respectively, IRSNB.FBL and UEANG.ODG. Ms Annelies Louage (MRAC.LI) worked at the

systematics lab of the SADC/GEF Lake Malawi/Nyasa biodiversity conservation project for three months in 1998. Dr Ngatinga of TANZ.FRI worked at MRAC.LI from 15 March to 4 April and from 9 to 14 October 2000. During these visits he re-identified shallow water *Lethrinops*, discussed his PhD thesis and concluded the description of a new species in press, and arranged the transfer of reference specimens to Africa Museum.

During the three major cruises of the project DC and EU scientists came together to work on the R/V Usipa and interacted together for about a two-week period. Short-term visits (up to 2 weeks) bilateral exchanges of staff occurred between UHULL and IRSNB.FBL to discuss protocols for the genetic work. Martin Taylor went to the molecular laboratory of the University of Hull to compare protocols on fragment length calling in macrosatellite studies. Microsatellite fragments that had been characterised in Brussels were rerun in Hull. Rizman Idid of Hull came to the molecular laboratory at the RBINS in order to discuss the various ways (i.e. exchange of unpublished sequences of potentially interesting outgroups) for the analyses of his mitochondrial DNA data set.

Although there were plans for more extensive exchanges of project staff among partners at the inception of the project these were not realized for a number of reasons: Opinions of MNRMW.FD.FRL and UMW.DB that funds were more effectively spent to support the research than travel and subsistence. As it turned out, other financial constraints materialised for MNRMW.FD.FRL. The planned visit by a scientist from IRSNB.FBL also did not happen owing to lack of funds. While the project coordinator made short visits to the laboratories of MNRMW.FD.FRL and UMW.DB, and to the Headquarters of TANZ.FRI in Dar es Salaam, planned visits in the last year of the project to Kyela in Tanzania and Metangula in Mozambique did not occur owing to unexpected illness which prevented travel to Africa for all of the last year of the project.

Problems

Project structure and funding

While the alteration to project structure suggested by MNRMW.FD.FRL made good scientific sense and was designed to provide a closer relationship between the Malawi Fisheries Research Unit (FRU) and the goals of the project, there arose significant problems with the movement of money from Fisheries Headquarters in Lilongwe to the FRU, who did the field work, based at the lake in Monkey Bay. Numerous attempts, including meetings with the, then, Chief of Fisheries failed to effectively resolve these difficulties. The difficulties were compounded both by the setting up of a foreign denominated bank account in dollars, to safeguard devaluation against the local currency, the kwacha, and by the apparent lack of funds required to keep a programme operational after the original advance of funds were used up.

The difficulties with cash flow is a general difficulty with DC partners. This problem was foreseen for TANZ.FRI and funds for day-to-day operations were provided through a sub-account by UDT.C.DZ. Such a strategy, however, places a significant extra demand on the project coordinator and requires the willingness of the coordinating institution to provide funds “up front” in order to enable the project to progress. Delays in providing verification of costs placed an extra and unnecessary burden on the project coordinator. The final difficulty that the project experienced

was that, in its efforts to fund an artisanal fisheries programme in Metangula, Mozambique it lost over US\$2000, which were disallowed as costs by the EC. Conditions in western Mozambique necessitated the project placing trust in representatives of Mozambique Fisheries. Although that representative did not follow agreed protocols, the loss does not lie with either the Mozambique Government but with UDTC.DZ. The EC should acknowledge that work in many DC countries requires an innovative approach and that the EC financial procedures may not always be appropriate to getting the work done. There needs to be a trust that things are done in good faith. Reporting to the EC about the theft (2nd annual report) elicited no response other than, subsequently, the rejection of costs in the 2001 cost statement. It should not be that partners are penalised for making supreme efforts to effect research in difficult conditions.

Timely delivery of reports and cost statements.

This was clearly a problem for some partners and for the coordinator in 2001 owing to illness. Other partners were always on time and provided clear and accurate costings. It is worth noting that late delivery of reports is not restricted to DC partners. Delays in financial and scientific reporting resulted in a delay of about one year in completion of the final report. Although there is no requirement within the protocols of the INCO programme, a representative of the project coordinator in the region for the whole duration of the contract would clearly have helped with effective management and timely delivery of reports and cost statements. In general, an overall recommendation for future INCO projects would be to have an officer with well-defined management responsibilities and scientific understanding, reporting directly to the project coordinator, to be based in the DC region for the duration of the project.

Subsistence costs.

The project budgeted for what it considered to be reasonable subsistence rates. Later in the project it transpired that the expected subsistence rates for travel abroad by DC Government officials was over US\$200 a day. It is a recommendation that in future projects the EC provide clear guidance on acceptable rates of subsistence, and that these guidelines are communicated via the project coordinator to all partners at the proposal stage.

REPORTS FROM PARTNERS IN THE PROJECT.

Partner 1: University of Dublin, Trinity College, Department of Zoology (UDTC.DZ)

Reporting Scientist: Kenneth Irvine

Other scientists involved: Patrick Buat (project), Patricia Ramlal, Stephanie Guildford (University Waterloo, Canada)

Objectives

UDTC.DZ was the lead partner for Task 1 (Project planning and coordination) and Task 2 (Primary photosynthetic and microbial production; through a sub-contract to the University of Waterloo, Canada). UDTC.DZ collaborated with partner 2 on Task 3 (quantification of benthic invertebrate communities), with partner 5 on Task 6 (fish diet analysis) and Task 8 (Trophic modelling), including quantification of *Chaoborus* diet.

Scientific activity report

Task 2. Primary photosynthetic and microbial production. The purpose of this task was to contribute to the development of a trophic model of the demersal fish production. Photosynthesis work was done through collaboration with the SADC/GEF Biodiversity Project that ran concurrently, for part of the project period, at the Senga Bay research station in southern Lake Malawi. Bacterial productivity in the lake and its relationship with benthic invertebrate communities was effected through a collaborative programme with and subcontract to the University of Waterloo, Canada. This involved estimation of bacterial activity at a number of depth profiles in the southern half of the lake.

Primary productivity is the energy base which sustains consumer populations, but bacterial production can play an important role in recycling organic carbon compounds into particulate forms available for consumer food webs (the microbial loop) and maintaining nutrients in the mixed layer for phytoplankton growth (Azam *et al.* 1983). Although primary production rates have been measured in most of the African great lakes, microbial production rates were previously unknown for Lake Malawi/Nyasa and rarely measured on the other African lakes. Because African lakes are continuously warm (>22 C) throughout their depths as well as throughout the year it might be expected that bacterial production rates in deep water columns (Cho and Azam 1988) might be a higher proportion of primary production than in other systems. In this study we report for the first time rates of bacterial production in Lake Malawi.

During June 1999 (cool, dry season) and January 2000 (warm, wet season), bacterial biomass and production were measured throughout the water column at two stations (respectively 150 m maximum depth, Lat 13 43 S, 34 40 E, and 180 m depth, Lat 13 30 S, Long 34 44 E) in the southern region of Lake Malawi/Nyasa. Bacterial production was measured using tritiated thymidine, following the method of Bell (1993). Briefly, water from various depths was incubated for 30 minutes with 20 nM

final concentration of methyl-³H thymidine. Thymidine incorporated into total macromolecules was extracted using cold trichloroacetic acid. Contemporaneous analyses were done for several factors of significance to bacterial growth. Bacterial cells were stained using the DNA stain 4',6-dimidino-2-phenylindole (DAPI) and counted using epifluorescence microscopy (Porter and Feig 1980). Bacterial biomass was calculated from appropriate geometrical models and cell measurements. Chlorophyll *a* was measured fluorometrically and suspended carbon using a CHN analyzer using the methods of Stainton *et al.* (1977). Temperature profiles were taken with a SeaBird 19 CTD.

Task 3. Diversity, structure, seasonality and production of invertebrates.

The assessment of benthic invertebrate community composition was supervised by partner 2 and is reported fully there. Production estimates of the invertebrates was within the project remit of UDTC.DZ. Pooled data from sixteen stations are reported on.

The role that bacteria and the so-called “microbial loop” have in lake trophic dynamics depends on rates of mineralisation of C and the factors that control that. It can be hypothesised that benthic invertebrates play a vital role in both mineralisation of C that has fallen as detrital rain from the water column and the fixing of that C into invertebrate biomass. The packaged C is then available for recycling in the lake, mediated by benthic feeding fish.

This hypothesis was investigated by a study that investigated:

- 1) Total organic matter (TOM) in the benthos at different depths;
- 2) The relationship between bacterial production and TOM; and
- 3) The relationship between bacterial production and invertebrate biomass in the sediment.

Samples for invertebrates, Total Organic Matter (TOM) content, and grain size were collected from throughout the lake using a PETITE PONAR sediment grab. Four grabs were taken at each station, of which one was sub-sampled for grain size and TOM and frozen immediately. The remaining three grabs were passed through an ENDICOTT sieve and material >212 µm fixed in 10% formalin for later sorting of invertebrates. In the laboratory, TOM was estimated from “lost on ignition” (Wetzel and Likens, 1991). Silt content was estimated as percentage total sediment dry weight of material that passed through a 63µm mesh sieve.

In the laboratory, invertebrates were removed, sorted and counted according to taxon using a binocular microscope. Estimates of biomass were obtained from loss on ignition. Benthic bacteria production was measured using the ¹⁴C-leucine technique following Moriarty (1990). A subsample of sediment is taken from the bucket using a microcorer made using a 3 ml plastic syringe with the tip cut and incubated with ¹⁴C-leucine for 30 minutes at room temperature (23°C), then killed with alcohol 80%. After 3 days at 4 °C the labelled bacteria were extracted from the sediment and the ¹⁴C measured with a LKB Wallac 1209 Rackbeta liquid scintillation counter.

Results Achieved

Task 2. Primary photosynthetic and microbial production.

Owing mainly to logistical difficulties there is very limited data on photosynthesis in the lake. Estimates (Guildford et al 1999), that come from the final report of the SADC/GEF Biodiversity Project (Bootsma and Hecky, 1999), are of average open-water photosynthesis rates of $1.75 \text{ mg C m}^{-3} \text{ hr}^{-1}$ in the upper layer of a station in the south-west arm the lake during 1997. Guildford *et al.* (1999) also reported estimates of benthic concentrations of chlorophyll *a*, sampled in November 1996, **that ranged from 75-176 $\mu\text{g l}^{-1}$, 58-122 $\mu\text{g l}^{-1}$ and 70-94 $\mu\text{g l}^{-1}$ at respectively, 2m, 5m and 10m depth.** Bacterial productivity in the lake and its relationship with benthic invertebrate communities was achieved through a subcontract to the University of Waterloo, Canada. This involved estimation of bacterial activity at a number of depth profiles in the southern half of the lake and was fully reported in the 3rd Annual report.

In June the water column was well mixed down to 80 m and only weakly stratified to 100 m during the course of the sampling at station 1. In January thermoclines were well established at both station 1 (mixed to 20 m) and station 2 at which the mixed layer depth deepened from 20 to 40 m between observations. Chlorophyll *a*, suspended C and bacterial biomass had higher values in the mixed layer in both months with the January samples being more strongly differentiated over depth especially in terms of bacterial biomass at station 2 (Table 1). This pattern resulted in a positive correlation between chlorophyll and bacterial numbers for all the data and a significant correlation between chlorophyll and bacterial biomass ($r = 0.6$, $p < 0.01$). In contrast, bacterial production showed no clear pattern with depth in June while in January the highest observed rate of bacterial production occurred at the deepest depth sampled (175 m at station 2). This high rate of production deep in the water column occurred at the lowest bacterial biomass observed in January implying that bacterial growth rates might also be high at the deeper depths. A similar pattern was observed at station 1 in January.

Bacterial biomass and particulate C concentration mean values were higher in the upper stratified column in January samplings than in June when the upper column was more deeply mixed (Table 1). January rates of bacterial production in the upper water column bracketed the June values in the upper water column while higher rates occurred deeper in the water column in January compared to June. Mean rates of bacterial production deep in the water column exceeded or were comparable with upper water column rates in these two periods of observation. From this limited sampling, mean bacterial production rates do not appear to vary greatly in Malawi although individual measurements can vary markedly (note standard deviations of the mean production rates in Table 2). The deeper water column rates occur in the presence of much lower chlorophyll and somewhat lower suspended C concentrations, which occur deeper in the water column. Because bacterial biomasses are lower at depths $> 50 \text{ m}$, bacterial growth rates may actually be higher at greater depths. Higher dissolved nutrient concentrations including organic substrates deeper in the water column may cause those higher rates. Table 2 shows comparisons of bacterial production rates estimated by thymidine uptake with those calculated from direct observations of increases in cell number and biomass over 24 hours (starting after an initial filtration through a $1 \mu\text{m}$ filter to isolate the bacteria from potential consumers). In June good agreement was found between the two methods of

measuring production, but in January the direct observations gave much higher estimates with a much higher standard deviation. In January, growth was dominated by rod shaped bacteria which were minor elements of the microflora in June and which did not grow over 24 hours in June. This change in the bacterial community, and the apparently rapidly growing rod shaped bacteria, was not reflected in the mean thymidine-based bacterial growth rate which was unchanged from June although the standard deviation of the January thymidine uptake measurements was higher than in June. More research will be required to resolve this anomaly. Lake Tanganyika and Lake Malawi have similar volumetric rates of bacterial production, and their mean rates are substantially higher than some warm marine systems (Table 3). Based on the published primary production, the African lakes and the marine systems have comparable rates of energy flow through the primary level, but the African lakes apparently sustain higher rates of bacterial production in the upper water column than the marine systems do. The African rates also sustain similarly high rates deeper in the water column. Over the maximum depth of these two stations in Lake Malawi (to 180 m), column integrated rates of bacterial production exceed the highest published annual rates of integral production for Lake Malawi. If only the upper water column is considered, the highest reported primary production rates in Malawi (Patterson and Kachinjika, 1995; Guilford *et al*, 2000) could sustain the rates of bacterial production observed. The highest reported annual rates of primary production in Malawi approximates the highest reported rates in Tanganyika (Sarvala *et al.*, 1999) which also has bacterial production rates similar to Malawi/Nyasa. However, given the evidence for high bacterial production rates occurring deeper in the water column (below 50 m) in both tropical lakes integral bacterial production may approximate integral primary production at certain times of the year when primary production is minimal. Much more frequent measurements of bacterial production over time and depth and contemporaneous measurements of primary production will be required to evaluate the balance of autotrophic and heterotrophic activity in the African Great Lakes.

Table 1. Mean, (s.d.), n for chlorophyll *a*, particulate carbon, bacterial biomass and bacterial production in the upper and lower water column at station 928, Lake Malawi in June 99 and January 00 and for station 900 in January 00.

Station	Date	Depth m	Chlorophyll <i>a</i> $\mu\text{g L}^{-1}$	Particulate Carbon mg L^{-1}	Bacterial Biomass mg C m^{-3}	Bacterial Production $\text{mg C m}^{-3} \text{ d}^{-1}$
1	June 99	< 50	0.60 (0.17) 9	148 (16) 6	3.42 (0.96) 6	8.1 (3.7) 18
1	June 99	>50	0.21 (0.12) 5	106 (17) 5	2.39 (0.69) 5	7.3 (3.7) 15
1	January 00	< 50	0.43 (0.24) 5	188 (42) 5	6.16 (1.37) 2	12.5 (7.7) 15
1	January 00	>50	0.05 (0.01) 2	145 (7) 2	1.09 (1.15) 2	10.4 (10.9) 6
2	January 00	< 50	0.54 (0.35) 5	220 (117) 5	10.3 (4.30) 2	4.8 (3.1) 15
2	January 00	>50	0.04 (0.02) 3	87 (15) 3	4.6 (5.7) 2	10.5 (2.6) 9

Table 2. Comparison of bacterial production measured using tritiated thymidine incorporation and increase in cell density.

Date	Bacterial Production mg C m⁻³ (Thymidine method)	Bacterial Production mg C m⁻³ (Cell count method)
June 99		
mean	9.00	9.53
s.d.	3.58	8.36
n	6	6
January 00		
mean	9.49	44.17
s.d.	5.55	43.40
n	8	7

Table 3. Comparison of bacterial and primary production for some systems with similar rates of primary production.

Lake/Ocean	Reference	Primary Production mg C m⁻² d⁻¹	Bacterial Production mg C m⁻³ d⁻¹
Lake Malawi	Bootsma 1993; Patterson and Kachinjika 1995	583-1420	-
Lake Malawi this study	Guildford (this study) < 50 m 50-170 m	-	8.5 9.4
Lake Tanganyika	Hecky and Fee 1981	700	-
Lake Tanganyika	Sarvala et al 1999 < 50 m 50 – 100 m	1265 - 1814	9 6
Mediterranean	Turley et al 2000 to deep chlorophyll maximum	151 - 502	0.4 – 1.0
Equatorial Pacific	Ducklow 2000 Euphotic	1083 - 1500	1.5 – 2.4
Arabian Sea	Ducklow 2000 Euphotic	1165	3.5

Task 3. Diversity, structure, seasonality and production of invertebrates.

The mean value of TOM in sediment ranged from < 1% dry weight at shallow stations to > 16% dry weight at deep stations, and increased with depth (Figure 1). Total densities of invertebrates decreased exponentially ($Y = 41.82e^{-0.028X}$) with depth from about 37,000 individuals m^{-2} at shallow depths to 760 ind. m^{-2} at 125 m station. Decrease in numbers of benthic invertebrates with depth varied among taxa (Figure 2). Molluscs and insects disappeared very quickly; present at 10 m but completely absent from sediment samples at 30 m. Other taxa were found at depths of 125 m. Bivalves, nematodes and chironomids were found in relatively high numbers, up to 2000 individuals m^{-2} , but all were completely absent in the sample collected from 200 m where only few *Chaoborus* larvae were found. Disappearance of most benthic invertebrates is likely to be related to oxygen availability. At depths below 175 m the water overlying the sediments can go anoxic and at depths > 130 m the concentration of oxygen is often < 2 mg $O_2 l^{-1}$.

Incorporation of ^{14}C leucine decreased from 5570 dpm ml^{-1} (0.0122 g C $m^{-2} d^{-1}$) at 8 m to 153 dpm ml^{-1} (0.0003 g C $m^{-2} d^{-1}$) at 180 m, with greatest difference in rate of incorporation found between 0 and 30 m (Figure 1). Sediment bacterial production (log transformed) decreased linearly ($r = 0.84$; $n = 5$; $P > 0.05$) but not significantly (n.b. low sample size) with increasing TOM. Sediment bacterial production increased ($r = 0.98$; $n = 5$; $P < 0.05$) with total invertebrate biomass. This relationship was significant but was heavily influenced by one high datum. Silt content increased from 5 % at 30 m to a 32 % at 75 m, with little further difference deeper than that (Figure 1).

Lake Malawi has rather low densities of benthic invertebrates, with total densities in the upper zones similar to the values obtain for the oligochaetes only in Lake Baikal (Martin *et al.*, 1999). Decrease of total densities appears as a monotonic decline with depth. Disappearance of invertebrates in deep zones is almost certainly a consequence of oxygen deficiency, although the gradual decline suggests that other factors are important above the zero oxycline. Rapid increase in silt content between 30m and 75m may reduce inhabitable space through compaction of the sediment, or limitation of chemical exchange may provide unfavourable conditions. Martin *et al.* (1998) showed that oxygenation in the sediment was reduced to the few first millimeters in shallow water and < 1 mm in deeper water above the anoxic layer. Decrease of total density of the benthic invertebrates may also reflect food availability (Pfannkuche, 1993) and high rates of decomposition in the warm waters of lake Malawi may reduce significantly the biotic material reaching the sediment in deep water.

Disappearance of invertebrates may be of some consequences for mineralisation of organic matter. Bacteria are the major processors in the mineralisation of C. It is uncertain why bacterial activity in the sediment decreased with increasing depth and appears, at first, to conflict with the findings (presented above) of highest bacterial production in the water column at the deepest sampling point of 175 m depth. Moreover, high silt content and high TOM values should favour bacterial production (Torreton *et al.*, 1997). An explanation of these results is that low numbers of invertebrates in the oxygenated demersal zone are, in fact, the cause of low bacterial activity found in the sediment. In marine waters, bacterial activity has been shown to be enhanced by invertebrates (Gerlach, 1978; Findlay and Tenore, 1982; Rieper-Kirchner, 1990; Alkemade *et al.*, 1992. Alkemade *et al.*, 1993 Parent and Morin, 1999).

Bioturbation by infauna may favour oxygenation and diffusion of chemicals into the sediment and enhance bacterial productivity (Alkemade, 1992). Benthic invertebrates may also “pre-digest” sedimented organic matter to provide a more suitable substrate for bacteria. Much organic matter reaching the sediment is likely to have been colonised and acted upon by pelagic bacteria. As depth of water above the sediment increases, the greater will be the bacterial activity on sedimented particles and the lower the C availability for subsequent bacterial activity. Use of remaining C requires further processing. Recycling of sedimented carbon can occur through invertebrate-mediated mechanical and chemical break-down of organic matter and release through faeces in a more accessible form.

The reduction of invertebrates in deep-water may limit pre-digestion, leaving benthic bacteria with a poor quality substrate. Low bacterial activity in deep water is supported by microscopic observations that at depths >125 m a great deal of terrestrial vegetation remains can be observed, such as rotten wood, leaves, and fibrous material.

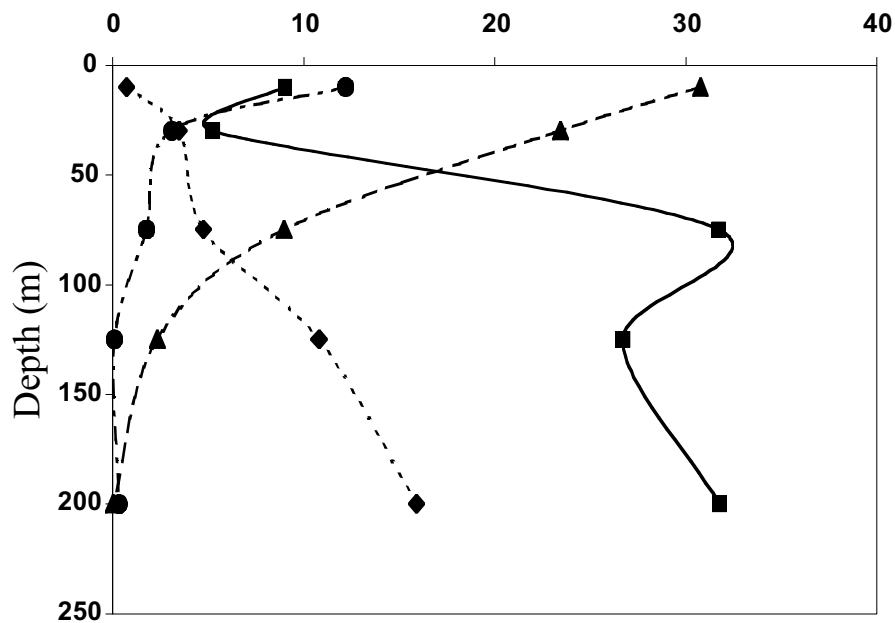
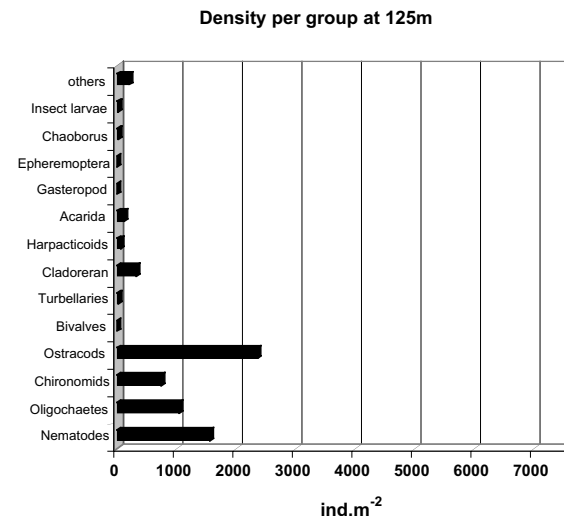
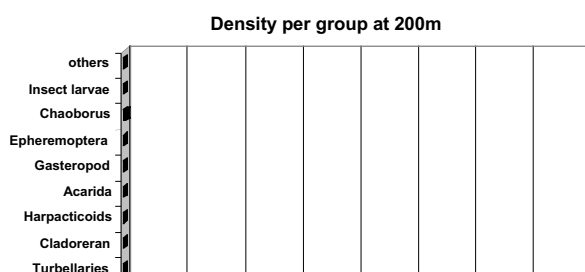
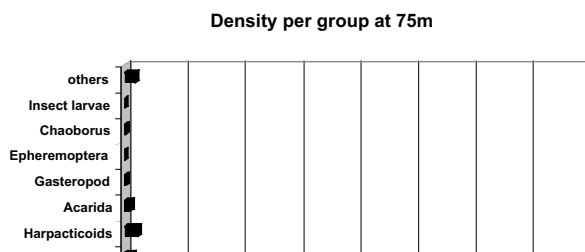
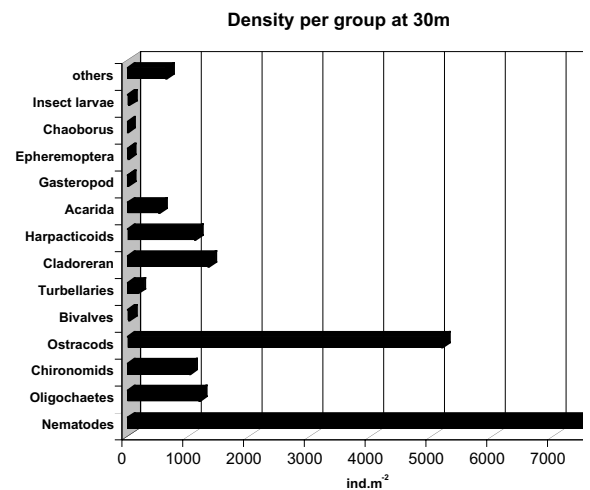
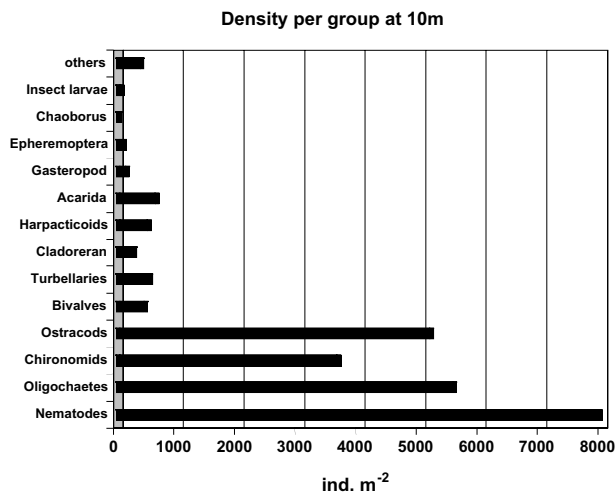


Figure 1. Total organic matter (TOM), ¹⁴C leucine incorporation by sediment bacteria, total invertebrate densities and silt content of sediments collected from various locations and depths in Lake Malawi

Overall, our results suggest that the deep benthos of Lake Malawi is limited primarily by physical conditions. In the deepest zones anoxic water limits availability of oxygen and provides a hostile environment for invertebrates. In deep oxygenated water limits to invertebrate production may be a combination of unsuitable physical structure and poor food supply. This, in turn, may limit bacterial productivity and provides a negative feedback to invertebrate production. This suggests that much of the demersal zone is a poor source of food for fish. Why that zone appears to support high densities of fish is, therefore, unclear and suggests the operation of other important mechanisms.

Problems encountered

Estimations of invertebrate densities and production rates were constrained by: 1) early methodological difficulties with the collection and sorting of invertebrates that arose from the frequency of fine sediment and generally low abundance of benthic invertebrates; 2) by limited opportunities to sample with suitable hydraulic gear; and 3) problems with infrastructure at the project base in Malawi which were accentuated by the absence of a permanent management structure and the short duration (ca 18 months) of UDTC.DZ project staff in Malawi. Mechanical breakdown of the R/V Usipa prevented *Chaoborus* feeding rate estimates but have been mitigated by use of previously collected data. Difficulties with the estimation of benthic invertebrate production rates have been dealt with by use of literature sources in the trophic modelling work. Overall, these problems restricted, but did not invalidate, the results that were obtained. On the other hand, the results that were obtained advance significantly our understanding of invertebrate community metrics and produced novel and exciting findings.



Publications and papers

- Buat, B, Ramlal P.S. and Guildford, S.J. (2002) The Relationship between Organic Matter, Invertebrates and Bacteria in the Sediments of Lake Malawi. *Journal of Aquatic Ecosystem Health & Management* 5: 307-314
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- Irvine, K. & K. Martens (2001). The Trophic Ecology of the Demersal Fish Communities of Lake Malawi/ Niassa, Central Africa. Bulletin for the International Decade for the East African Lakes, Spring 2001: 5, 10.

Conclusions

The project collected information for the first time on bacterial production in Lake Malawi and provided the most extensive coverage to date of benthic invertebrate populations in the lake. Both of these studies provided findings highly relevant to the trophic dynamics of Lake Malawi and, through inference, to other deep water tropical lakes. The work fed directly into data requirements for a trophic model of the demersal fish community on the lake, reported on by partner 5. Although the extent of the data collected was more limited than we had anticipated it, nevertheless, provides an important contribution to the understanding of ecological pathways affecting the fisheries production of the lake.

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Partner 2: The Royal Belgian Institute of Natural Sciences (RBINS.FBL)

Reporting Scientist: Kenneth Irvine

Other scientists involved: Patrick Buat (project), Patricia Ramlal, Stephanie Guildford (University Waterloo, Canada)

Task 3: taxonomy of invertebrates

Reporting scientist: Koen Martens

Other scientists involved: Patrick Buat (project), Kelly West (3rd party contracts)

Objectives

RBINS.FBL provided a base-line revision of literature on the benthic invertebrate fauna of the Lake Malawi/Nyassa and provided an identification guide to the benthic invertebrates of the lake under task 3 of the project. A separate team reported under task 4 (see below)

Scientific activity report

Putative records of all non-insect invertebrate groups from Lake Malawi and associated waters were checked in the Zoological Record. Papers were then requested from the library and were checked individually. Taxonomic lists of non-insect invertebrates thus known to have been found in or around the lake were compiled. Specialists then screened these lists for potential synonyms and obsolete nomenclature. Benthic samples were taken on several cruises parallel to trawls for demersal fish. The extant diversity of two groups (Mollusca and Ostracoda) was determined from a subset of these samples to test how representative the list of published records is. New taxa of Ostracoda were illustrated using Scanning Electron Microscopy. Based on the extant groups, a key to the major invertebrate groups was drafted; illustrations are from published records.

Results achieved

Invertebrate diversity in Lake Malawi

More than 300 non-insect invertebrate species in about 160 genera have been reported from the lake and associated water bodies (Table 4). The majority of the species occurs in the lake itself, which thus has a high standing diversity. Most of these records, however, are old (< 1950) and identifications are therefore not always trustworthy. This is especially true for groups of small animals, such as Rotifera. Several higher taxa which are present in, for example, Lake Tanganyika are absent from Malawi, the most noteworthy being the Cnidaria and the Hirudinea.

Table 4: Non-insect invertebrate diversity in lakes Nyasa/ Malawi and Tanganyika. Data for Lake Malawi original, abstracted from the literature, except for Ostracoda which include new records. Data for Tanganyika modified from Coulter (1991, 1994) for ostracods using data of Wouters & Martens (2001). L= lacustrine, A = Associated water bodies, T= total. Species scored for both L and A are referred to L.

Taxon		Malawi				Tanganyika			
		genera	species			genera	species		
			L	A	T		L	A	T
Cnidaria		0	0	0	0	2	1	1	2
Porifera		2	2	0	2	6	7	2	9
Bryozoa		0	0	0	0	6	6	0	6
Mollusca	Gastropoda	9	22	5	27	36	24	36	60
	Bivalvia	5	10	1	11	10	7	8	15
Nematoda		6	3	5	8	12	4	16	220
Nematomorpha		0	0	0	0	12	20	0	20
Acanthocephala		0	0	0	0	3	9	0	9
Pentastomida		0	0	0	0	1	1	0	1
Gastrotricha		3	0	5	5	0	0	0	0
Rotifera		33	37	40	77	25	9	61	70
Annelida	Oligochaeta	9	?	?	9	7	9	0	9
	Hirudinaea	0	0	0	0	8	20	?	20
Plathelminthes	Cestoda	0	0	0	0	6	8	0	8
	Turbellaria	0	0	0	0	2	2	0	2
	Trematoda	2	0	3	3	3	3	0	3
Tardigrada		1	1	0	1	0	0	0	0
Crustacea	Decapoda (Caridea)	1	1	0	1	5	14	1	15
	Decapoda (Brachyura)	1	4	0	4	1	8	2	10
	Branchiura	3	4	0	4	3	9	4	13
	Ostracoda	21	57	6	63	21	82	18	100
	Copepoda (Calanoida)	2	6	0	6	1	1	0	1
	Copepoda (Cyclopoida)	13	13	10	23	11	36	3	39
	Copepoda (Harpacticoida)	6	6	7	13	6	16	0	16
	Copepoda (parasitic)	6	16	0	16	5	4	8	12
	'Cladocera'	28	?	?	52	19	6	18	24
	Isopoda	0	0	0	0	1	3	0	3
	Conchostraca	1	0	1	1	0	0	0	0
	Bathynellacaea	1	0	1	1	1	1	0	1
Arachnida	Acarina	7	5	9	14	21	24	22	46
TOTAL		160	187	93	341	234	334	200	734

Ostracod diversity

Close to one hundred benthic samples were taken in the lake, using several methods: dredge, PONAR grab and hand net using SCUBA. Five of the richest dredge samples were analysed for their ostracod diversity (Table 5).

Table 5: Localities and samples from which ostracods have been identified. Samples are qualitative and were selected because they were the richest with thousands of specimens. CTY= country, MOZ= Mozambique, MAL= Malawi.

Sample	Station	S°	S'	S''	E°	E'	E''	Date	CTY	Locality	Depth (m)	Method
LM/99/01	LM/01	12	38	531	34	46	685	21.3.99	MOZ	Metangula	8	dredge
LM/99/02	LM/01	12	38	537	34	46	345	21.3.99	MOZ	Metangula	30	dredge
LM/99/03	LM/02	11	20	71	34	49	628	23.3.99	MAL	Mbamba Bay	7	dredge
LM/99/04	LM/03	13	26	307	34	22	530	25.3.99	MAL	Domira Bay	11	dredge
LM/99/05	LM/04	14	18	395	35	9	149	26.3.99	MAL	S.E. Arm	10	Dredge

The diversity found was very high: where previously only 20 species had been reported (mostly from associated water bodies), no less than 40 species, all lacustrine, can now be added to the list, bringing the total to 60 . Of these, at least 35 are new species, more than half of which belong to at least two new genera (Figs 3-5). 62% of the species are endemic to the lake and surrounding waters. The main radiations are in Cypridopsinae (18 new species in at least one new genus), *Limnocythere s.l.* (10 new species in several genera, some possibly new), *Gomphocythere* (4 new species) and finally a new cypridid genus, tentatively placed in the Cyprinotinae (3 new species). The 6 *Chrissia* species are not endemic to the lake and moreover are mostly found from associated water bodies; they are not considered as a lacustrine species flock of this lake.

Number of ostracod species per sample was also high, ranging between 8 and 14, but the number of shared species and similarity indices are low (Table 6). Interestingly, depth seems to be more important than location with regard to similarity of (ostracod) fauna. Whereas samples 1 and 2, from the same locality (Metangula, Mozambique, at 8 and 30 m respectively), have zero similarity, samples 1 and 5, with comparable depth but 300 km distance from each other, have the highest similarity index (Table 7).

Table 6: Species list of Ostracoda from Lake Malawi and adjacent waters. Bold names are new records of the present project. Litt.= literature record

Physocypria	castanea	litt.	Cypridopsinae n.gen.	sp. L n.sp.	3
Cypria	lenticularis	litt.	Cypridopsinae n.gen.	sp. M n.sp.	2
Candonopsis	africana s.l.	1,5	Cypridopsinae n.gen.	sp. N n.sp.	2
Ilyocypris	propinqua	1,3,5	Cypridopsinae n.gen.	sp. O n.sp.	1,3
Oncocypris	mulleri	litt.	Cypridopsinae n.gen.	sp. P n.sp.	4
Chrissia	sinuata	litt.	Cypridopsinae n.gen.	sp. Q n.sp.	5
Chrissia	marginata	litt.	Cypridopsinae n.gen.	cunningtoni	litt.
Chrissia	perarmata	litt.	Zonocypris	costata	1,5
Chrissia	fulleborni	litt.	Cypridopsis	vidua	litt.
Chrissia	fasciculata	litt.	Plesiocypridopsis	fulleborni	litt.
Chrissia	stagnalis	litt.	Gomphocythere	sp. 1 n.sp.	3,4,5
Stenocypris	major	litt.	Gomphocythere	sp. 2 n.sp.	1
Acocypris	platybasis	litt.	Gomphocythere	sp. 3 n.sp.	2
Strandesia	laticauda	litt.	Gomphocythere	sp. 4 n.sp.	4
Cypricerus	inermis	litt.	Limnocythere	jocquei	Litt.
Neocypridella	fossulata	litt.	Limnocythere s.l.	sp. 1 n.sp.	2
Humpheycypris	sp. 1	5	Limnocythere s.l.	sp. 2 n.sp.	1
cyprinotinae n.gen.	sp. 1 n.sp.	2,4	Limnocythere s.l.	sp. 3 n.sp.	1,3
cyprinotinae n.gen.	sp. 2 n.sp.	3,5	Limnocythere s.l.	sp. 4 n.sp.	1
cyprinotinae n.gen.	sp. 3 n.sp.	5	Limnocythere s.l.	sp. 5 n.sp.	3
cypridopsinae n.gen.	sp. A n.sp.	1	Limnocythere s.l.	sp. 6 n.sp.	3
cypridopsinae n.gen.	sp. B n.sp.	1	Limnocythere s.l.	sp. 7 n.sp.	3
cypridopsinae n.gen.	sp. C n.sp.	5	Limnocythere s.l.	sp. 8 n.sp.	5
cypridopsinae n.gen.	sp. D n.sp.	1	Limnocythere s.l.	sp. 9 n.sp.	5
cypridopsinae n.gen.	sp. E n.sp.	3	Limnocythere s.l.	sp. 10 n.sp.	5
cypridopsinae n.gen.	sp. F n.sp.	1,4,5	Alicenula	serricaudata	2
cypridopsinae n.gen.	sp. G n.sp.	1,4,5	Alicenula	inversa	(5)
cypridopsinae n.gen.	sp. H n.sp.	1	Darwinula	stevensoni	2
cypridopsinae n.gen.	sp. I n.sp.	3	Penthesilenula	gr. incae	3
cypridopsinae n.gen.	sp. J n.sp.	2,4	Cypridopsinae n.gen.	sp. O n.sp.	1,3
cypridopsinae n.gen.	sp. K n.sp.	3	Cypridopsinae n.gen.	sp. P n.sp.	4

Table 7: Total number of species per sample (bottom line), number of shared species (left side of table) and similarity index (right side of table) between the 5 analysed samples in Table 2. Similarity index $S = 2C/A+B$ where C = number of shared species, A= number of species in sample A and B = number of species in sample B (Odum, 1971). E= Eastern side of the lake, W= western side of the lake, S = South Eastern end of the lake.

Samples	1(E)	2(E)	3(W)	4(W)	5(SE.)
1		0.00	0.23	0.19	0.36
2	0		0.00	0.27	0.00
3	3	0		0.11	0.23
4	2	2	1		0.29
5	5	0	3	3	
TOTAL	14	8	12	7	14

Mollusc diversity

The mollusc fauna of Lake Malawi and associated water bodies is taxonomically revised (West, 2001 – see appendix). In total, 38 mollusc species in 14 genera have thus far been reported from Lake Malawi, 55% of the species are endemic to the lake and/or associated water bodies. Similar to the approach for ostracods, molluscs were identified from several rich dredge samples from the S.E. Arm of the lake (locality LM/99/05 in Table 2). Five gastropod species and 4 bivalve species were found (Table 8). None of these species and genera were new. This indicates that the mollusc fauna of Lake Malawi is reasonably well-known, at least compared to smaller groups, such as ostracods.

Table 8: Molluscan species identified from a dredge sample from S.E. Arm of Lake Malawi (loc. LM/99/05 in table 5).

Gastropods:	Bivalves:
Bellamya capillata	Spatharia (Spathopsis) nyassaensis
Bellamya robertsoni	Caelatura hypsiprma
Lanistes nasutus	Caelatura nyassaensis
Lanistes nyassaensis	
Melanoides tuberculata	
Bivalves:	
Aspatharia (Spathopsis) nyassaensis	
Caelatura hypsiprma	
Caelatura nyassaensis	
Mutela alalta	

A key to the invertebrates of Lake Malawi

Based on the literature survey, a list of extant aquatic groups was drafted and a preliminary identification key to these groups was made. This key was tested in actual field conditions and several improvements were included during the course of the project. It was found that a pictorial key would work best. In the version attached here (appendix 1), a dichotomous descriptive key, illustrated with habitus images (important features are arrowed) allows identification of the major groups. Non-dichotomous, pictorial treatments of two case-studies, Ostracoda and Mollusca, are also provided.

Discussion

Invertebrate diversity

Thus far, 341 species, representing 187 genera, of non-insect invertebrates have been reported from Lake Malawi and adjacent waters; 55% of these species occur in the lake itself. Lake Tanganyika has about twice that diversity, with 734 species, representing 234 genera, and 45.5% of the species being lacustrine. At least part of this difference is due to a differential research effort, as Lake Tanganyika has received more taxonomic attention over the past decade than any of the other African lakes. The major part of species reported from Lake Malawi date from before 1950, whereas several dozen more recent papers report on Tanganyikan invertebrates. Nevertheless, the difference in specific and generic invertebrate diversity most likely also reflects a reality. Tanganyika is a much older lake than Malawi. Although age of species flocks and age of lakes are not necessarily correlated (i.e. species flocks can be either younger or older than the lake itself), longevity of a lake basin is reflected in standing diversity, in this case in absolute numerical diversity (Martens et al., 1994; Martens, 1994, 1997).

However, basin age also correlates to percentage endemism and to the highest taxonomic rank of endemism. For example, more than 50 % of the total number of species reported from Lake Baikal (25-30 million years old) and surrounding waters is endemic; while this is only 11% of the species from the much younger Lake Titicaca (c 3 million years old) (Table 9). Total specific endemism in Lake Malawi remains as yet unknown, but in ostracods, for example, 62% of all species (lacustrine or not) are endemic (c 70% and 86% in Tanganyika and Baikal respectively).

Table 9: Summary of total and crustacean (specific) diversity and endemism in three long-lived lakes. Compare % crustacean diversity and endemism. (after Martens & Schön, 1999).

Diversity & endemism	Baikal	Tanganyika	Titicaca
Total specific diversity	1901	1290	533
Crustacean diversity	613	219	70
% Crustacea	32	17	13
% total endemism	52	49	11
% crustacean endemism	72	58	27

Also, Lake Baikal has an endemic family of Amphipoda, whereas the much younger lakes Ohrid and Titicaca, both with significant amphipod radiations, have at most endemic genera. Similarly, an endemic ostracod tribe (Tanganyikacypridini in Megalocypridini) occurs in Lake Tanganyika. Thus far Malawi only has a few endemic genera. The relevance of levels of diversity and endemism to lake management is discussed below.

Some higher taxa are seemingly absent from Lake Malawi, for example Cnidaria and Hirudinea. This most likely reflects the paucity of research efforts for such groups. It is almost impossible that the cnidarian *Hydra* would not occur in at least some associated waters. Also several Hirudinea must occur, but so far this group was not investigated in Lake Malawi. The absence of the Tanganyikan medusae is, on the other hand, established and significant.

Ostracod and mollusc diversity in Lake Malawi

In order to assess the knowledge of the extant diversity of Lake Malawi invertebrates, two model groups were here studied in some more detail. These groups, Mollusca and Ostracoda, were chosen because both are believed to be diverse and important for the ecology of most ancient lakes (Martens, 1997). The preliminary assessment of the diversity of both groups yielded some surprising results. Firstly, it appears that the specific diversity of Ostracoda is considerably higher than that of Mollusca (60 versus 38 species), but levels of specific endemism are similar (62 compared with 55 % respectively). Secondly, whereas a preliminary survey of lacustrine habitats added no less than 40 ostracod species to the fauna of Lake Malawi, with 35 being new to science, no new species of molluscs were found in a comparable survey (if only the SE Arm sample is taken into account, still 10 new species of ostracod were found). It will take a long time to prepare formal descriptions of all of these ostracod taxa. Therefore, a preliminary atlas of these species is offered in addendum, so that future taxonomic and ecological work on Lake Malawi can refer to these species with their 'monikers'. The present assessment of Malawian Mollusca does not imply that no new molluscan species will be discovered in the lake. The present results indicate, however, that compared with other invertebrates, molluscs are well-known and are thus a reliable group to use for ecosystem studies and monitoring programmes.

Thirdly, an assessment of the different ostracod radiations in different lakes shows that although Malawi shares some of its lineages with Tanganyika (Limnocytheridae, Cypridopsinae), some important Tanganyikan lineages are completely missing from Malawi (Candonidae, Cytherideidae). This demonstrates the dual signal provided by such comparative analyses amongst lakes. On the one hand, certain groups do appear to be pre-adapted to thrive and speciate in ancient lakes. On the other hand, serendipity is also potentially important in determining which groups arrive in the lakes on time to establish viable populations and lineages. Note, also, that the correlation between taxonomic group and longevity of the basins postulated by Martens (1994) is here corroborated, as only the oldest lakes Baikal and Tanganyika have extensive radiations of Cytherideidae, while these are absent in younger lakes, such as Malawi. In Molluscs, the family Thiaridae has a limited radiation in Lake Malawi (9 species in 1 genus), but an extensive one in Tanganyika (more than 40 species in several genera).

Finally, a preliminary analysis of diversity and similarities between the investigated stations indicates that depth is more important in determining similarities between faunas than geographical location, even when stations several hundreds of kilometers apart are compared. This result should of course be interpreted with caution, as sample size is very limited and thus this interpretation can only be regarded as a testable working hypothesis. Nevertheless, the results are compatible with the known palaeolimnological history of the lake, which has shown considerable lake level fluctuations during its history. This must have caused significant faunal migration, across the N-S gradient of the lake, i.e. along the Eastern and Western shores, but also across the lake. When hyper arid periods caused low lake stands, the northern basin dried up completely and faunal exchanges were possible along the northern side of the southern basin. Note, also, that due to its bathymetry, Malawi never fell apart into isolated basins, as Lake Tanganyika did (Coulter, 1994). There was, thus, less opportunity for allopatric speciation and a higher faunal similarity across the lake is thus more plausible in Lake Malawi.

Relevance of diversity data for lake management

Ancient lakes are hotspots of biodiversity and endemism and the present data support this conclusion for Lake Malawi, not only for the already well-documented case of the fish family Cichlidae, but also for a wide range of invertebrate groups. Of certain groups, such as the Ostracoda, only a fraction of the extant diversity appears to be known. Further taxonomic and ecological studies of invertebrate groups are thus urgently required.

The importance of biodiversity for ecosystem functioning is a heavily debated, but highly relevant subject. For example, although ecology of endemic invertebrate species remains ill known (even worse than their taxonomy), there seems to be a considerable number of redundant species in these ecosystems. Indeed, niche diversification between 15 ostracod species found sympatrically on the same sandy patch appears low. Redundancy can be a buffering mechanism against species loss in (more or less predictable) fluctuating environments. Cyclic changes in physical limnology and lake levels at Milankovich time scales have been documented for both Lake Tanganyika and Baikal. Such environmental alterations are bound to affect lacustrine ecosystems. A large number of species per functional guild will allow species loss without ecosystem-collapse. Conservation programmes should thus not focus exclusively on keystone taxa and function, but should rather manage aiming for redundancy as a buffer for ecosystem resilience to both climatic or human induced disturbances (Martens, in press).

Also, at least some indications of niche diversification are found with regard to bathymetric distribution. As invertebrates are a very important food source for fish (see report of UEANG.ODG), it is important to know which invertebrate species occur where in the lake and under which conditions. For most invertebrate groups, such as ostracods, not even the basic data on diversity and autecology are available, the lack of these important data will hamper scientific management.

Two of the important achievements of task 3 of the present project are that (1) it presents a baseline study of invertebrate diversity of the lake and (2) that it provides tests of the robustness of these data for two independent model groups. It appears that

Mollusca, a food group for the adults of a specialised group of cichlids, are well-known and lake-wide surveys should not encounter vast taxonomic problems. However, for smaller groups such as the ostracods which are an important food group for benthic juvenile fish, surveys are seriously hampered by taxonomic problems. Results of Task 3 (see report UDCT.DZ) show that small groups are indeed important, as they occur in large densities (e.g. more than 5000 individuals m⁻² at 10 m and still more than 2000 individuals m⁻² at 125 m). At least for the ostracods, the atlas presented here will allow identification of an important part of the fauna of lake Malawi.

Problems encountered

The collection of the necessary literature was a very time-consuming occupation. Older references, which constitute the majority of papers reporting on Lake Malawi invertebrates, cannot be screened with electronic search engines. The literature search thus required laborious checking of more than 100 years worth of volumes of the Zoological Record (and this for more than 10 major groups), after which hundreds of papers were requested from various libraries. These papers had then to be screened meticulously and records extracted. All of this required years of technical work and was primarily executed by permanent staff of the R.B.I.N.Sc., not by the project itself. However, this baseline study will now stand for all future research on Lake Malawi.

Sampling was hampered by various technical problems, arising from the fact that (1) during cruises, priority needed always to be given to trawling of demersal fish; (2) reliance on extra-project logistics (eg. of GEF) made that regular sampling was not always possible and (3) various logistic problems in the field (laboratory space, availability of power, etc.) prevented efficient sorting of the samples. Again, several months worth of sampling was executed by staff of the RBINS.FBL amongst others the samples studied for ostracod faunas. Taxonomic work on the new material, for ostracods but also for other sorted groups, is preliminary, due to the unexpected (based on the literature survey) high diversity. However, this rich material will be the bases for many years of future taxonomic studies. Already, a paper describing 5 new species of *Gomphocythere* (Ostracoda, Limnocytheridae) is *in press*.

Finally, because of all of the above, the key to the invertebrates of Lake Malawi has been tested in the field on less occasions than was originally anticipated. Nevertheless, these “test ID-sessions” have already lead to significant improvements of the key, which can now also be used by non-specialist biologists.

Publications and papers

- Martens, K. & I. Schön 1999. Crustacean biodiversity in ancient lakes: a review. In: Danielopol, D.L. & K. Martens (eds.), “Crustacean Biodiversity in Subterranean, Ancient/Deep Lakes and Deep-Sea Habitats”, *Crustaceana* 72(8): 899-910.
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Conclusions

The research on the taxonomy of invertebrates of Lake Malawi during the present project has been successful, and this in spite of some logistic and other difficulties. Both objectives have been met: A baseline study of published records of Malawian invertebrate species has been conducted and the lists have been updated to present-day taxonomy by specialists; and a key to the major groups of Malawian invertebrates has been produced, tested and refined. In addition, the discovery of 35 new species of Ostracoda from lacustrine habitats in Lake Malawi is astonishing and this material will be the basis for ongoing studies for several years to come and Mollusca have been established in Lake Malawi as a fairly well-know group which can be incorporated within future ecosystem monitoring programmes.

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Task 4. Genetics data to support fish taxonomy

Reporting Scientists: Erik Verheyen and Martin Taylor

Objectives

The goal of the research activities carried out by this partner was to provide information concerning the levels of population substructuring in *Copadichromis* sp. 'virginalis kajose', a demersal cichlid fish species from Lake Malawi; maintain a dialogue with collaborating partners in the fish genetics work, including the determinations of the choice of microsatellite and mitochondrial DNA sequences

Scientific Activity Report

The objective was reached within the projected 11 months period (01/03/1999-2000) during which additional labour (Dr. Martin Taylor) was contracted to carry out this work at the Molecular laboratory of the Royal Belgian Institute of Natural Sciences. Fish samples were collected (Figure 3) during a fieldtrip to lake Malawi (25/9-10/10/1998 & 3/9/99-15/9/1999).

Materials and methods

Choice of model species.- Among all demersal cichlid species from Lake Malawi that are of potential economic importance for the trawling fisheries on the lake we were advised by Dr. Jos Snoeks from the 'Fish taxonomy team' to select *Copadichromis* sp. 'virginalis kajose'

Sample collection. - A total of 280 *Copadichromis* sp. 'virginalis kajose' were collected from demersal trawl samples taken on Lake Malawi in 1998 and 1999. Additional samples were donated by the Global Environment Facility Lake Malawi Biodiversity project. All samples were trawled at between 50 and 75 metres depth over an area of approximately 1500 metres length, with a minimum of 45 and a maximum of 72 individuals per population. Tissue samples were preserved in 100% ethanol and stored at room temperature until their arrival in the laboratory, where they were stored at 4°C.

DNA preparation and amplification. - Total DNA was extracted from ethanol preserved fin clips using Proteinase K digestion and salt precipitation, following a protocol modified from Aljanabi & Martinez (1997). Extracted DNA was resuspended in 200µl of autoclaved Milli Q H₂O.

Microsatellites. - All samples were screened for variation at each of 6 SSR loci, 4 of which are perfect dinucleotide repeats (Pzeb1, Pzeb3 (van Oppen *et al.*, 1997b), UNH002 (Kellog *et al.*, 1994), and UNH130 (Lee & Kocher, 1996)), 1 imperfect dinucleotide repeat (Pzeb5 (van Oppen *et al.*, 1997b)), and one compound repeat (Pzeb4 (van Oppen *et al.*, 1997b)). PCR amplifications were performed under the following conditions: 94°C 120s, followed by 5 cycles of 94°C 45s; 55°C 45s; 72°C 45s. followed by 30 cycles of 91°C 30s; 55°C 30s; 72°C 30s. followed by 72°C 10

minutes. 10µl reaction mixes consisted of 2µl (≈20ng) template DNA, 0.5 µM of each primer, 200µM of each dNTP, 0.26 units Taq polymerase (Pharmacia Biotech), 1µl 10x reaction *buffer* (Pharmacia Biotech). The mixture was overlaid with 10µl of mineral oil. Amplified products were resolved on 6% denaturing polyacrylamide gels (short) on an Alf Express DNA sequencer (Pharmacia Biotech). Product sizes were determined by comparison with M13 mp8 DNA size standards, following van Oppen *et al.* (1997b). Allelelinks software (Pharmacia Biotech) was used to size the fragments. Allele sizes given were rounded up to the nearest allele.

Mitochondrial DNA sequencing. - PCR's were performed in 25 µl volumes consisting of 2.5µl of Taq buffer (Pharmacia Biotech), 0.2 mM of each dNTP, 0.4 µM of each primer, ~50 ng of template DNA, and 0.65 units of Taq polymerase (Pharmacia Biotech). The temperature profile for the PCR was 94°C 60s; 52°C 60s; 72°C 90s for 30 cycles. The PCR products were purified using the Easyprep (Pharmacia Biotech) system prior to cycle sequencing. Cycle sequencing was performed according to the manufacturers protocol (Pharmacia Biotech), using 0.8 µM primer, 2.5 units of Taq polymerase and approximately 0.15-0.2 µg of the PCR product. The temperature profile for the cycle sequencing reaction was 95°C 36s; 52°C 36s; 72°C 80s and after 25 cycles the samples were kept at 72°C for 5 min. The samples were denatured at 95°C for 3 minutes before running on a 6% polyacrylamide gel using an ALF or Alf Express DNA sequencer (Pharmacia Biotech).

Data analyses

Microsatellites. - Genotypes at all pairs of loci were tested for linkage disequilibrium (between each pair of loci in each population) and deviations from Hardy-Weinberg equilibrium using the exact test of GENEPOP (GENEPOP version 3.1d; Raymond & Rousset, 1995). Significance levels were determined using the Markov chain method. Due to the continuing debate over the most suitable mutation model for microsatellite data, population differentiation was calculated using both the infinite allele model (IAM, Kimura & Crow, 1964), and the stepwise mutation model (Ohta & Kimura, 1973; Kimura & Ohta, 1978). Population differentiation was therefore tested in three different ways. Fisher's exact tests (which does not assume a mutation model) were used to **test for differences in allele frequencies between populations using GENEPOP 3.1d (Raymond & Rousset, 1995). FST was estimated by _ (Weir & Cockerham, 1984) using ARLEQUIN (Schneider *et al.* 1997), and unbiased RST (Slatkin, 1995) was calculated using RST CALC (Goodman, 1997). The values from the three statistics were tested for significant departures from zero using permutation tests contained in the respective packages.**

True breeding null alleles (alleles that cannot be amplified owing to mutations in the primer binding sequence) have been detected in Lake Malawi cichlid fishes by previous workers (van Oppen *et al.*, 1997a). For the few individuals for which PCR products could not be generated for a single locus after two or three attempts were considered to be homozygous for a null allele.

MtDNA data analysis. - Haplotypes were assigned on the basis of discrete nucleotide sequences. An exact test for differences in haplotype frequency between populations with was performed with 10,000 Markov Chain steps using ARLEQUIN 1.1 (Schneider *et al.*, 1997).

Results achieved

Microsatellites.- All loci were polymorphic for all the populations sampled. For the five populations combined, the mean number of alleles per locus varied from 5 in Pzeb5 to 37 in Pzeb1. Mean H_e per locus ranged from 0.32 in Pzeb5 to 0.95 in Pzeb1. Within sample H_e ranged from 0.70 for Chilola to 0.79 for Domira and Mbamba Bay. Observed and expected heterozygosities per sample, allele number, size ranges and significant deviations from Hardy-Weinberg expectations are shown in Table 10. There was no evidence of linkage disequilibrium in any pair of loci ($P > 0.05$). Deviations from Hardy-Weinberg expectations were tested using Fisher's exact test. After Bonferroni correction (Rice, 1989), 5 of the 30 pairwise tests revealed significant deviations from equilibrium. Four of these were at Pzeb1, and one at Pzeb4. Previous studies (van Oppen *et al.* 1997a) have detected true breeding null alleles at Pzeb1, and this is a likely cause of significant heterozygote deficiencies. The inclusion of this locus in the analyses did not significantly change the estimates of population structure, so we elected not to remove it from the analyses.

Over all samples, F_{ST} gave highly significant levels of intersample genetic variance. The overall F_{ST} () estimate was 0.004, $P = 0.003$, bootstrapping over loci. R_{ST} (RHO) gave a higher, and statistically more significant estimate: R_{ST} (RHO) = 0.019, $P < 0.00001$, (averaging over loci).

Multilocus estimates of exact tests revealed highly significant differences between Cape Maclear and Mbamba Bay, Cape Maclear and Chilola and Cape Maclear and Metangula. Results from exact tests on single loci, reveal that 3 loci, Pzeb1, Pzeb4 and UNH130 are responsible for all of the significant differences between samples (Table 11). Cape Maclear was found to be significantly differentiated from Mbamba Bay, Metangula and Chilola using F_{ST} . Only Cape Maclear and Metangula were significantly differentiated using R_{ST} after Bonferroni correction (Table 12). Domira Bay was found to have significantly different allele frequencies to Metangula using multi locus exact tests, significant differentiation was also apparent using F_{ST} and R_{ST} (Table 12). There was no evidence of any correlation between genetic and geographic distance between samples. Mantel tests on pairwise matrices of R_{ST} and F_{ST} were all non-significant ($P > 0.05$).

MtDNA. - We identified 7 distinct haplotypes and 6 polymorphic sites among 329bp of the mtDNA Dloop in 20 *C. sp. 'virginalis kajose'* specimens collected from 3 sites, Domira Bay, Cape Maclear and Chilola (Table I). Haplotype A was observed in all three populations with frequencies ranging from 0.6 to 0.8. Haplotypes B, C, D, and E were only found in a single individual each in the Cape Maclear population. Haplotype F was found in a single individual in the Domira population and haplotype G was found in a single individual in the Chilola population. An exact test revealed no significant differences in haplotype frequencies between populations ($P > 0.05$).

Discussion

Comparison with other Malawi cichlids. - This is the first study to investigate population substructuring in any species of demersal cichlid fish. Microsatellite DNA markers reveal small but significant levels of population substructuring over all populations ($F_{ST}=0.004$, $P=0.002$; $R_{ST}=0.019$, $P<0.00001$). This structuring was low and over a much larger geographic scale when compared with previously published studies of the mbuna (rock-dwelling species), but greater than that found in pelagic cichlid species inhabiting Lake Malawi.

Microsatellite allele frequencies were compared with previous studies on the mbuna, and found to be similar to those found by van Oppen *et al.*, (1997) for the Pzeb loci, but slightly larger for locus UNH002 (34 in comparison with 24 found by Arnegard *et al.*, 1999 and 29 found by Markert *et al.*, 1999). Variation was also very similar to that found in pelagic cichlid species (Shaw *et al.*, 2000). Comparing F_{ST} estimates between other groups of Lake Malawi cichlids and *C. sp. 'virginalis kajose'* is therefore statistically valid.

Levels of population differentiation have been estimated for several species of mbuna using microsatellite loci (van Oppen *et al.*, 1997a; Arnegard *et al.*, 1999; Markert *et al.*, 1999). These studies revealed extremely high levels of population structuring at very fine geographic scales. F_{ST} estimates calculated for populations of four species of mbuna separated by 700-1400 metres by van Oppen *et al.* (1997a) were between $(_) = 0.007$, $P<0.01$, and $(_) = 0.015$, $P<0.001$. Far higher estimates of population substructuring were calculated for two further mbuna species on a larger geographic scale (42 km), $(_) = 0.063$, $P=0.0002$ and $(_) = 0.151$, $P<0.0002$ (Arnegard *et al.*, 1999; Markert *et al.*, 1999). The overall level of substructuring in *C. sp. 'virginalis kajose'* ($F_{ST}=0.004$, $P=0.0008$) is considerably lower than found in the two largest geographic scale mbuna studies (Arnegard *et al.*, 1999; Markert *et al.*, 1999), but only slightly lower than estimates from van Oppen *et al.* (1997a). However; the geographic scale of the current study was an order of magnitude larger than the Arnegard *et al.* (1999) and Markert *et al.* (1999) studies, and several orders of magnitude larger than the van Oppen *et al.* (1997) study. In addition to research on the mbuna, a recent study on pelagic cichlid species inhabiting Lake Malawi (Shaw *et al.*, 2000) using both microsatellite and mitochondrial sequence data revealed no evidence of population substructuring on a lakewide scale. The levels of structuring found were between one order of magnitude ($F_{ST}=0.0003$) and 3 times smaller ($F_{ST}=0.0012$) than the levels found in the current study. Thus, the level of substructuring found in the current study for the demersal cichlid, *C. sp. 'virginalis kajose'*, falls between the highly stenotopic, rock-dwelling mbuna, and the open-water pelagic species.

These differences in levels of substructuring between the groups, may influence, or have influenced, the speciation mechanisms responsible for their diversification. The very high levels of population substructuring found in the mbuna, which inhabit the highly fragmented rocky shoreline, favours an allopatric origin for many of these species. In contrast, Shaw *et al.* (2000) suggest that the apparent monophyly of both the pelagic groups of species, coupled with minimal population substructuring and lack of physical barriers to migration is consistent with a sympatric origin for the pelagic species. The intermediate level of substructuring found in *C. sp. 'virginalis*

kajose', with the northern and southern populations exhibiting significant substructuring, is consistent with allopatric divergence. However, the lack of differentiation between geographically less distant populations does not necessarily exclude sympatric scenarios.

Despite the evidence that population substructuring occurs on a relatively large scale (in comparison with the mbuna), the possibility of much finer population differentiation cannot be ruled out. Constraints imposed by trawl sampling preclude the capture of individuals from highly localised areas. However, sampling at different times of the year suggests fine scaled structure is unlikely. *C. sp. 'virginalis kajose'* was absent from sites (Metangula and Mbamba Bay) in September in which they were present in March (unpublished data). This was unlikely to be merely a depth change, such as moving to shallow waters to breed, as they were absent from all depths trawled (10m-100m). Although the possibility that they may have been present at depths between the trawl samples, or at less than 10 m, cannot be discounted, this suggests some local movement does occur.

Comparison with other demersal habitats.- In many respects the demersal habitat of Lake Malawi bears more resemblance to a marine environment than to many freshwater habitats. The distances between populations can be quite large, and there are no obvious physical barriers constraining migration. Comparing the levels of substructuring found in the current study with 14 cod populations (*Gadus morhua*), reveals an overall F_{ST} value of (0.0084, $P < 0.001$) (Ruzzante *et al.*, 1998), more than twice that found in the current study ($F_{ST} = 0.004$, $P = 0.002$). However, the cod study was over an area of approximately 3000km, whereas the current study is over an area of approximately 250km. The lack of a pelagic dispersal phase and a low fecundity may allow substructuring to occur at much smaller geographic scales (<300km) than are typically found in marine demersal habitats.

Potential influence of lake water level on population structure. - Lake Malawi is known to have undergone at least two major reductions in lake level in the past 50,000 years (Scholz & Rosendahl, 1998; Gasse *et al.*, 1989. Owen *et al.*, 1990; Tiercelin & Mondegeur, 1991). A drop of 100-150m below its present level is likely to have occurred between 6,000 and 10,000 years BP, and more recently, a similarly sized drop may have occurred between 500 and 200 years BP. There is no evidence that Lake Malawi was split into separate basins during these arid periods (which would have require a drop of more than 400m), which suggests that the population structuring observed in the present study has arisen within the confines of the current lake basin. This is in contrast with Lake Tanganyika which has been split into separate basins at least twice in its history (Verheyen *et al.* 1996). This is reflected in marked genetic discontinuities which correspond to the low-level lake basins in some of the cichlid species inhabiting Lake Tanganyika.

Implications for fisheries.- Although the levels of population substructuring between populations are low, the data presented here have implications for fisheries practices on the lake. At present, all commercial trawling is conducted over a very limited area in the south-east arm of the lake (Turner 1996). Intense fishing pressure may deplete populations at a faster rate than can be balanced by immigration from surrounding populations, leading to reduction in population size, and reduction in genetic diversity.

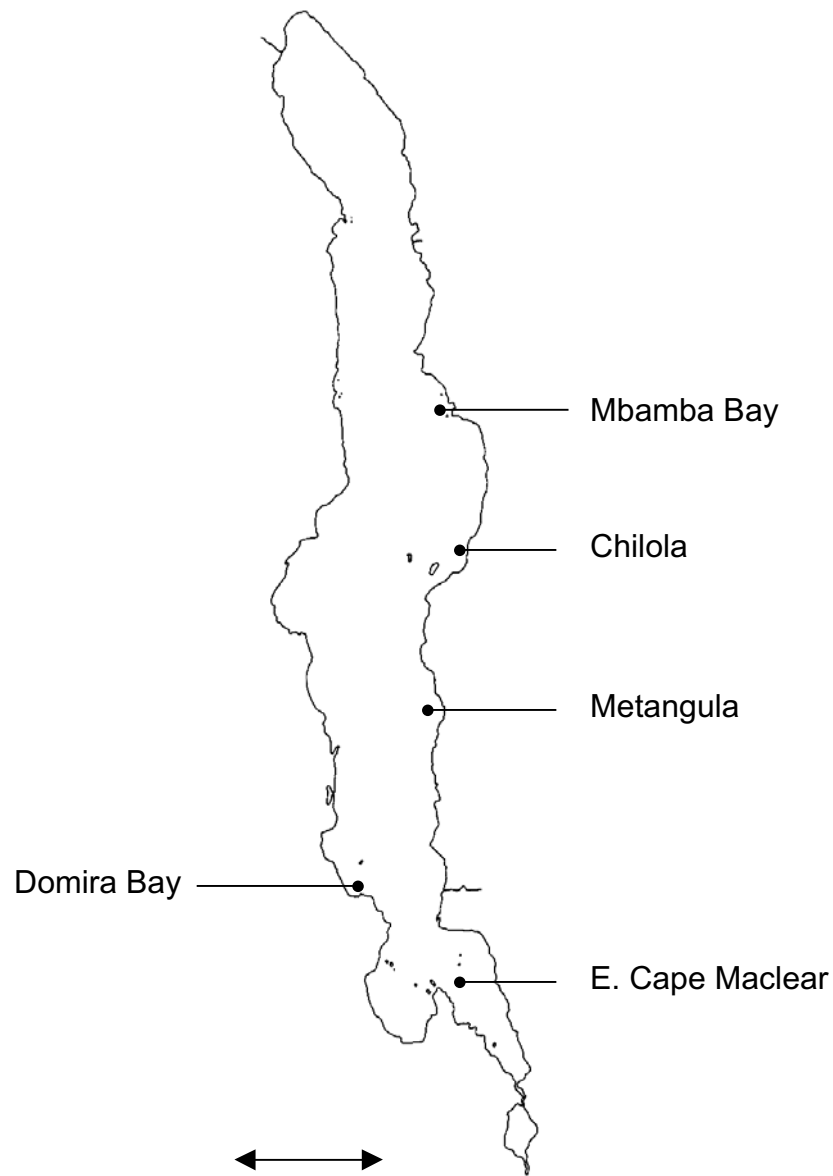


Figure 3. Fish collection sites of RBINS.FBL in the current study.

Table 10. Genetic variation at 6 microsatellite loci within 5 populations of *Copadichromis* sp. ‘*virginialis kajose*’.

		Population					Averages
		Domira Bay (n=45)	Mbamba Bay (n=72)	Metangula (n= 67)	Cape Maclear (n=49)	Chilola (n=47)	
Pzeb1	No. of alleles	28	42	36	42	35	37
	Allele size	126-210	124-228	120-218	120-238	122-218	120-238
	He	0.95	0.96	0.95	0.97	0.95	0.95
	Ho	0.84*	0.81*	0.74*	0.88	0.75*	0.80
	Null	0.05	0.08	0.11	0.05		
Pzeb4	No. of alleles	17	18	19	15	16	17
	Allele size	113-167	113-163	113-167	113-153	113-151	113-167
	He	0.88	0.90	0.85	0.82	0.79	0.85
	Ho	0.80	0.88	0.79	0.86	0.60*	0.79
	Null	0.05	0.01	0.03	0.00		
Pzeb3	No. of alleles	7	11	11	11	7	9
	Allele size	308-326	312-340	312-336	306-332	314-336	306-340
	He	0.62	0.67	0.65	0.67	0.59	0.64
	Ho	0.62	0.57	0.61	0.55	0.54	0.58
	Null	0.06	0.06	0.05	0.09		
Pzeb5	No. of alleles	6	5	6	6	4	5
	Allele size	123-135	127-139	115-131	121-133	121-131	115-139
	He	0.39	0.31	0.29	0.35	0.24	0.32
	Ho	0.36	0.31	0.25	0.35	0.25	0.30
	Null	0.03	0.00	0.19	0.05		
UNH002	No. of alleles	28	30	34	34	25	30
	Allele size	161-231	165-235	165-241	163-235	165-273	161-273
	He	0.93	0.93	0.95	0.94	0.80	0.91
	Ho	0.82	0.87	0.92	0.92	0.65	0.83
	Null	0.07	0.03	0.02	0.03		
UNH130	No. of alleles	37	37	36	33	32	
	Allele size	162-246	162-244	160-242	166-246	166-274	162-274
	He	0.97	0.94	0.96	0.95	0.85	0.93
	Ho	0.89	0.91	0.85	0.88	0.77	0.86
	Null	0.04	0.022	0.062	0.052		
Mean no. alleles		21	24	24	24	20	
Mean He		0.79	0.79	0.77	0.78	0.70	
Mean Ho		0.72	0.72	0.69	0.74	0.59	

* denotes a significant deviation from Hardy-Weinberg equilibrium after sequential Bonferroni correction.
‘Null’ indicates the estimated number of null alleles for each population at each locus using the maximum likelihood algorithm in GENEPOP 3.1 d (Raymod & Rousset, 1995).

Table 11. Tests of differences in microsatellite allele frequencies between all pairs of samples.

	Cape Mac.	Domira Bay	Metangula	Chilola	Mbamba Bay
Cape Mac.		PZ1*, UNH130*	PZ1**, PZ4***, UNH130*	PZ4***	PZ1*, PZ4***
Domira Bay	NS		UNH130*	PZ4**	NS
Metangula	<<0.001	0.002		NS	PZ1**, PZ4*
Chilola	<<0.001	0.016†	NS		PZ1*, PZ4*
Mbamba Bay	<<0.001	NS	0.008†	NS	

Above diagonal: Individual loci exhibiting significant differences (*P<0.05, **P<0.01, ***P<0.001). Below diagonal: Multi locus probabilities of homogeneity (†=values that become non-significant at Bonferroni corrected significant value of P<0.005).

Table 12. F_{ST} () and R_{ST} estimates for all pairs of samples.

		F _{ST}				
		Cape Maclear	Domira Bay	Metangula	Chilola	Mbamba Bay
	Cape Maclear		0.000	0.009***	0.011***	0.007***
	Domira Bay	0.024**†		0.003	0.002	0.001
RST	Metangula	0.040***	0.019**†		-0.003	0.002
	Chilola	0.018*†	0.001	0.007		-0.001
	Mbamba Bay	0.016*†	0.011*†	0.017**†	0.013*†	

*P<0.05, **P<0.01, ***P<0.001 (†=values that become non-significant at a Bonferroni corrected level of P<0.005).

Problems encountered

The sampling programme that was realized for the genetics part of the project should have been considerably more extensive in terms of number of investigated species and numbers of localities from different areas in the lake. It is indeed likely that the information that the three partners involved with the genetical aspects of project have been able to provide to the partner involved in the ecological modelling should have been more representative for the fish fauna that is exploited. The reason that not more species from more areas in the lake were studied is due to a combination of the taxonomical knowledge on this fauna and the abundance of the known species in the catches. Ideally the investigated species needed to be taxonomically very well known as well as to have a (almost) lake-wide distribution range. Unfortunately, the combination of these two criteria were only met for the selection of species investigated during this project.

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- Taylor, M.I., Rüber L. & Verheyen E. (2001). Microsatellites reveal high patterns of population substructuring in the species-poor Eretmodine cichlid lineage from Lake Tanganyika. *81th ASIH/AES Meeting, Penn State University, Pennsylvania, USA*

Conclusions

This is the first study to investigate population substructuring in any species of demersal cichlid. Small but significant differences were found in microsatellite allele frequencies between five populations investigated. Estimates of population substructuring revealed significant differences between some, but not all populations. The overall F_{ST} estimate was (F_{ST})=0.004, $P=0.002$. The overall R_{ST} estimate was (R_{ST})=0.019, $P<0.00001$ (averaging over loci). The mean number of microsatellite alleles per locus ranged from 5 to 37, resulting in an overall expected heterozygosity of 0.32 to 0.95. The study suggests that there is low but significant levels of genetic substructuring in this demersal species. This information was provided to other partners involved in the project in order to be built into the ecological model.

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Partner 3: Africa Museum (MRAC.LI)

Task 4: Fish taxonomy, morphology

Reporting scientists: Jos Snoeks & Mark Hanssens

Objectives

As stated in the technical annex, the task of the museum (partner 3) was to take charge of the fish taxonomy part and to closely integrate with other partners during survey work, and especially with the partners involved in the genetic work.

The fish taxonomy work (task 4) was to contribute to existing studies on the biodiversity of the lake, and would concentrate on the species of numerical or biomass importance. Reference collections were to be deposited in local and international museum/research institutes.

Scientific Activity Report

Material and methods

We have used the standard methods of modern cichlid taxonomy, i.e. the study of colour patterns and morphometrics combined with univariate and multivariate data analyses (Snoeks, 1994, 1999). An extensive summary of the methods and techniques used was given in the first annual report. Figure 4 represents an illustration of the major measurements used in this study. In total, some 23 measurements and 18 meristics were taken from each individual examined, complemented with several qualitative observations. Multivariate techniques used were primarily Principal Component Analyses (PCA); non-parametric, distribution-free tests such as the Mann-Whitney U test were used for univariate comparison.

Results achieved

Revision of some problematic deep-water Lethrinops taxa

This was the first group specifically studied for this project. It is one of the major groups targeted by deep-water fisheries and the taxonomy is very complex. At the same time, this study very well complemented a then ongoing study on the shallow-water *Lethrinops* by Ben Ngatunga and Jos Snoeks (Ngatunga & Snoeks, 1999; Ngatunga, 2000). The study was executed by Annelies Louage (Africa Museum) and Jos Snoeks (at that time still affiliated to the SADC/GEF project). The taxa examined were the *L. longimanus-macracanthus-mylodon* group, the *L. gossei*-complex and the *L. longipinnis*-complex. Based on re-identifications of the collections at Senga Bay, distribution maps were plotted for all taxa examined.

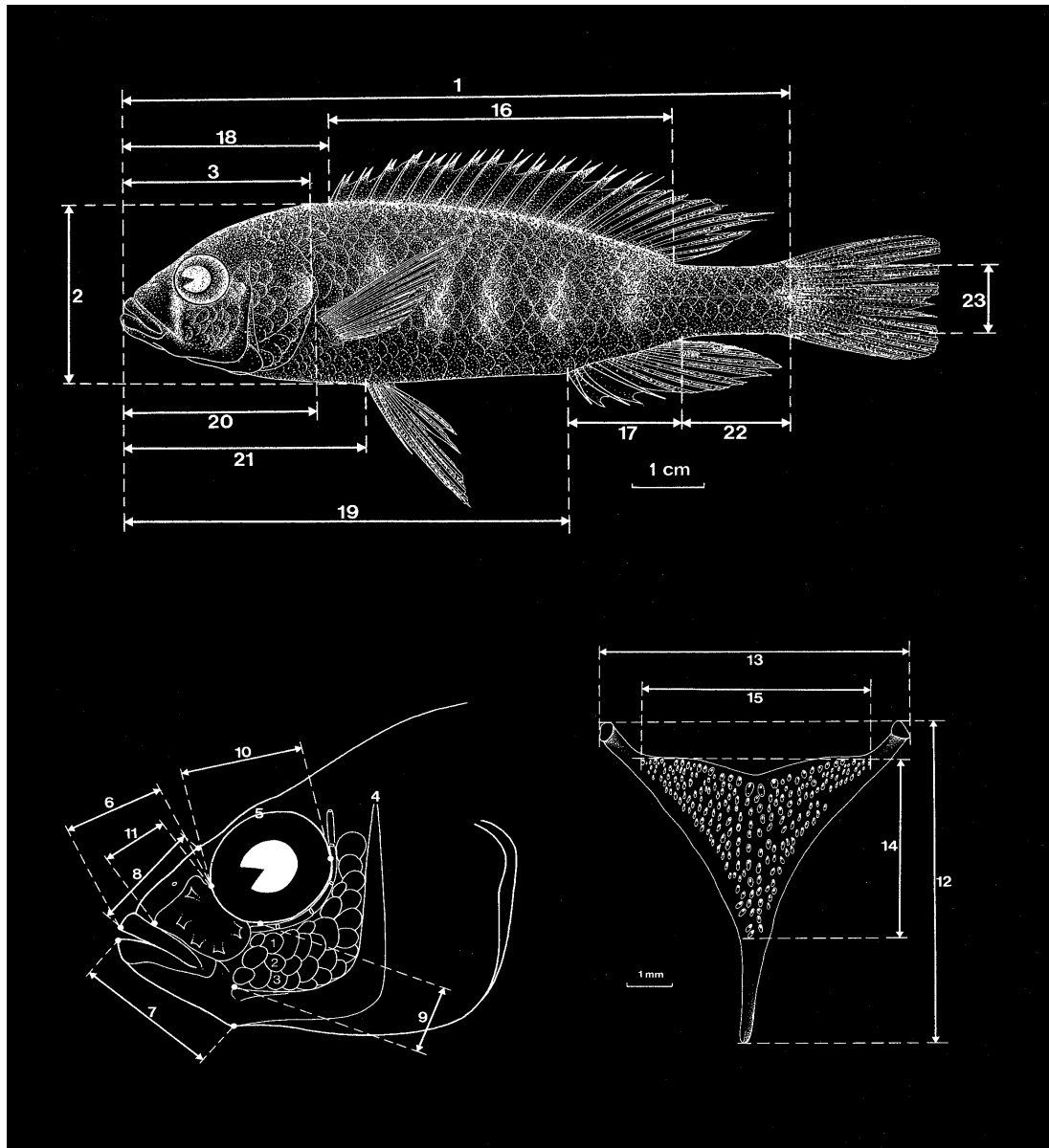


Figure 4: Schematic representation of body, head and lower pharyngeal jaw measurements.

The species of the *L. longimanus-macracanthus-mylodon* group are very similar in overall habitus. They all possess a short snout, with a terminal mouth set low on profile (Eccles & Lewis, 1979). Based on our analyses, we could distinguish them clearly (Table 13, Figure 5).

Table 13: Discriminating features between *L. longimanus*, *L. macracanthus* and *L. mylodon* (modal numbers in bold).

Species	<i>L. longimanus</i>	<i>L. macracanthus</i>	<i>L. mylodon</i>
Pharyngeal bone	Normal	Normal	Very enlarged
Pharyngeal teeth	Enlarged or molariform	Some enlarged	Very molariform
Anal fin base	20.4 (19.0-21.3) % SL	22.9 (22-24.3) % SL	20.2 (17.8-21.0) % SL
Gill raker number	14-15- 16 -17-18-19	21 -22-24	11-12- 13 -14

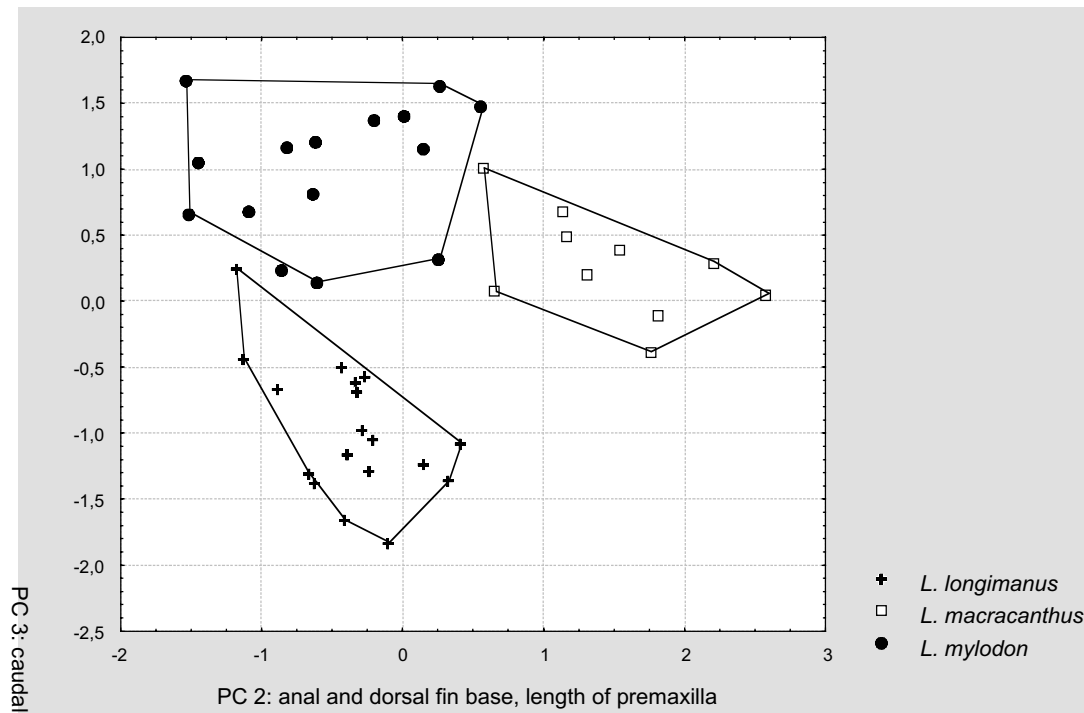


Figure 5: Scatterplot of scores on the second and third axis of a PCA of log-transformed measurements of all specimens examined of the *L. longimanus-macracanthus-mylodon* group.

The existence of two subspecies within *L. mylodon* could not be confirmed owing to the lack of specimens from the type locality of *L. mylodon borealis*. In contrast we did discover geographic variation between the populations from the north and northwest compared with those from the south and south-eastern parts of the lake for *L. longimanus* (Table 14). These observations need further elaboration to find out whether or not *L. longimanus* as currently defined is polyspecific.

Table 14: Discriminating features between *L. longimanus* from the south and south-east and *L. longimanus* from the north and north-west. (modal frequencies in bold).

	<i>L. longimanus</i> (N.-NW.)	<i>L. longimanus</i> (S.-SE.)
Length of premaxilla	33.3 (32.3-35.7) % SL	31.7 (30.4-33.6) % SL
Length of caudal peduncle	17.5 (16.1-18.5) % SL	18.7 (17.8-20.5) % SL
Number of gill rakers	17-18-19	14-15- 16-17

Lethrinops sp. ‘deep-water albus’ is a species that is morphologically closer to *L. longipinnis* than to *L. albus* itself. Within what is regarded as *L. longipinnis*, we could detect four different species, based on a thorough multivariate analysis (Table 15). Most probably *L. sp. ‘longipinnis orange head’* corresponds to *L. argenteus*, a species known only from four types from the northern part of the lake.

Table 15: Distinctive features between *L. sp. ‘deepwater longipinnis’*, *L. sp. ‘longipinnis orange head’*, *L. sp. ‘longipinnis white lappets’* and *L. longipinnis* (modal frequencies in bold).

Species	<i>L. sp. ‘deepwater longipinnis’</i>	<i>L. sp. ‘longipinnis orange head’</i>	<i>L. sp. ‘longipinnis white lappets’</i>	<i>L. longipinnis</i>
<u>Pharyngeal teeth</u>	Fine	Mostly enlarged	Mostly fine	Fine or some enlarged
Gill raker number	9	9-10-11	7-9-10	9-10
Caudal peduncle depth	12.5 (11.7-13.1) %SL	12.5 (12.0-13.6) %SL	13.6 (13.0-13.9) %SL	12.7 (11.5-13.7) %SL
Head length	38.6 (37.8-40.0) %SL	35.8 (34.3-37.5) %SL	37.1 (35.6-38.5) %SL	37.1 (35.8-38.6) %SL

A small study on the deep-water *L. altus*-group clearly revealed the need for a more detailed study of the generic relationships between the shallow-water and deep-water *Lethrinops* and *Placidochromis*. Certainly some deep-water species put in the genus *Lethrinops* do not have the typical *Lethrinops* dentition.

Geographic variation in Mylochromis anaphyrmus

This study was executed by Mark Hanssens and Jos Snoeks, the former as a contractor for extra labour. *M. anaphyrmus* was chosen for this study as a representative of the shallow water demersal community. It was one of the target species for life-history studies within the project. In this study, four populations of *M. anaphyrmus* were compared from the southern and central parts of the lake. We found a clear sexual dimorphism, i.e. morphological differences between males and females in this species.

There are small but significant morphological differences among all *M. anaphyrmus* populations examined. The results of one of the analyses are illustrated in Table 16. The amount of difference is clearly linked to geographical distance. These results confirm the genetic structuring that was found between the same populations (Duponchelle, et al. 2000) and are also suggestive of restricted gene flow between these populations. Populations in this species are, therefore, not part of a large uniform 'stock' but are separated by restricted gene flow.

Table 16. Results of Mann-Whitney U-tests on males of the four populations of *M. anaphyrmus* examined. Above diagonal, number of significantly different measurements and p values. Below diagonal, p value for SL and number of specimens used. SWA = South West Arm, DOMB = Domira Bay, KOTA = Nkhotakota, CHIN = Chinteché.

	SWA	DOMB	KOTA	CHIN
SWA	-	2 p<0.05	3 p<0.05 1 p<0.005	4 p<0.05 3 p<0.005
DOMB	p = 0.52 n SWA = 19 n DOMB = 10	-	1 p<0.05 1 p<0.005	3 p<0.05 1 p<0.005
KOTA	p=0.86 for SL n SWA = 9 n KOTA = 9	p = 0.56 n DOMB = 8 n KOTA = 9	-	1 p<0.005 1 p<0.0005
CHIN	p=0.46 for SL n SWA = 18 n CHIN = 16	p=0.93 n DOMB = 6 n CHIN = 12	p = 0.52 n KOTA = 10 n CHIN = 14	-

The *Copadichromis virginalis* complex

This study has been executed by Mark Hanssens and Jos Snoeks, the former as a contractor for extra labour. The genus *Copadichromis* was erected by Eccles & Trewavas (1989) to accommodate the group of *Utaka* as revised by Iles (1960). These are one of the economically more important fish groups of the lake (Chisambo, 2000). One of the new species described by Iles (1960) was *C. virginalis*. He reported that two different morphs were found at the type locality, Nkhata Bay. The holotype and some paratypes belong to the deep-bodied form, locally referred to as 'kaduna', while some other paratypes are more elongated and locally named 'kajose'. Iles (1960) stated that these two forms at the type locality could be taken to represent two sympatric and closely related species, easily separated on the basis of several characters (among which body depth). However these forms appeared to be more difficult to distinguish at other localities where intermediates occurred. Since he was unable to analyse populations from other parts of the Lake, he considered it best to regard the Nkhata Bay forms as belonging to one species. This state of affairs has obviously complicated the identification of the species; hence the data in fisheries statistics, reports and scientific publications referring to *C. virginalis* have to be interpreted with caution. In addition, *C. mloto*, another 'utaka' similar to but more elongate than the kajose form *C. virginalis* has been mixed with the latter (Turner, 1996; Snoeks, pers. obs.). Turner (1996) reported on *C. virginalis* as the eight most

abundant taxon in his 1992 survey, comprising almost 4% of the total sample weight. It often dominated catches, on occasion comprising 86% of the sample weight.

The aim of this study was to study the geographic variation in *C. ilesti* (which was considered identical with the *C. sp.* ‘virginalis kajose’ form), as a complement to the study by Taylor & Verheyen (2001; and see genetics report RBINS.FBL) on the population substructuring based on microsatellite data. However, taxonomic problems were found when comparing the *C. ilesti* types with the ‘kajose’ types. Therefore, first, a more elaborate study was started involving the three species in the *C. virginalis* complex (*C. virginalis*, *C. sp.* ‘virginalis kajose’ and *C. ilesti*) and, subsequently, the geographic variability in *C. sp.* ‘virginalis kajose’ was analysed.

We found three distinct species within the *C. virginalis* complex. *Copadichromis ilesti*, which was believed to be conspecific with the ‘kajose’ types of *C. virginalis* (Konings, 1999) appeared to be distinct. Pending its formal description, the ‘kajose’ form of *C. virginalis* should therefore be referred to as *C. sp.* ‘virginalis kajose’. *Copadichromis virginalis* can relatively easily be distinguished from the other two species by its deeper body and smaller size at maturity. The two elongate species, which are of similar body shape and size at maturity can be distinguished on the basis of other characters.

Mann-Whitney U tests were used to compare *C. sp.* ‘virginalis kajose’ with *C. ilesti* (*C. virginalis* could not be compared with these two species due to the large size differences). To exclude allometric inferences, for this comparison a selection of specimens of similar SL was used (Table 17).

Table 17. Results of the Mann-Whitney U tests between *C. sp. 'virginalis kajose'* (n=15) and *C. ilesi* (n=11); n.s. = not significant, + = $p < 0.05$; ++ = $p < 0.005$; +++ = $p < 0.0005$; p-value for standard length = 1.0.

Lachrymal depth % HL	n.s.
Snout length % HL	+++
Lower jaw length % HL	+++
Premaxillary pedicel length % HL	+
Cheek depth % HL	+++
Eye diameter % HL	n.s.
Interorbital width % HL	n.s.
Interorbital width % HW	n.s.
Head width % HL	n.s.
Head length % SL	+
Body depth % SL	++
Dorsal fin base % SL	+
Anal fin base % HL	+
Predorsal distance % SL	++
Prepectoral distance % SL	n.s.
Preventral distance % SL	n.s.
Preanal distance % SL	n.s.
Caudal peduncle length % SL	+
Caudal peduncle depth % SL	++
Caudal peduncle depth % CPL	++

Copadichromis ilesi has a larger cheek depth, snout length and lower jaw length than *C. sp. 'virginalis kajose'*. In addition, *C. ilesi* has a larger, stronger and more procumbent outer oral dentition than *C. sp. 'virginalis kajose'*. The gape of *C. ilesi* is less inclined, 30-35° to the horizontal vs 45° in *C. sp. 'virginalis kajose'*. There appear to be ecological differences as well. *Copadichromis virginalis* and *C. sp. 'virginalis kajose'* are demersal sand-dwelling species, and are mostly collected by bottom trawling, up to great depths. *Copadichromis ilesi* has been reported to be associated with rocks, and has been collected at very shallow depths (Konings, 1999).

Geographic variation in *C. sp. 'virginalis kajose'* was analysed using PCA and Mann-Whitney U tests. For convenience, we delimited four geographic regions. The South (SO) comprised both transects, the SW Arm and the Nankumba Peninsula; the Central East (CE) included Chilola and Chiwanga; the Central West (CW) included Nkhata Bay; the North East (NE) contained Iwela and Manda. In the PCA, the specimens from the two northern localities came out as most distinct, but owing to the small sample size and the difference in absolute size compared with the other populations, these differences could not be analysed further. Based on the Mann-Whitney U tests, further differences were found between the specimens from the other three regions. The largest difference (9 out of 20 of measurements significantly different) was found between the SO and CW specimens. This confirmed the results of the PCA, in which

CW was slightly separated from the other two regions. Only two significant differences were found between CE and either SO or CW.

Based on a population-level study on microsatellite DNA analyses, Taylor and Verheyen (2001) concluded that *C. sp. 'virginalis kajose'* does not comprise one single lake-wide population, but that it is divided into smaller subpopulations that exchange relatively few migrants. Our morphometric results demonstrate that this population substructuring is also found within the species' morphology.

The pattern found in *C. sp. 'virginalis kajose'* differs from the results on four populations of *Mylochromis anaphyrmus*, a shallow-water demersal cichlid (Duponchelle, et al., 2000; see above). In *M. anaphyrmus*, more significant morphological differences were found among the four populations examined. These differences were found between populations at much smaller distances (four localities on the West coast, between SW Arm and Chinteché, South of Nkhata Bay), and were clearly related to distance; the more distant the populations, the more and the larger were the morphological differences. Populations of *M. anaphyrmus*, therefore, seem to be more isolated than those of *C. sp. 'virginalis kajose'*. *M. anaphyrmus* is found in shallow water where rocky shores may be effective barriers to the migration of this sand-dwelling species. *C. sp. 'virginalis kajose'* is found in deeper waters where no physical barriers are known and where migration between populations can be larger.

Deep-water Placidochromis

During the SADC/GEF Lake Malawi/ Nyasa Biodiversity Conservation project, a new sub-flock of deep-water dwelling, closely related, small to medium-sized cichlids was discovered, which are tentatively placed in the genus *Placidochromis*. (Hanssens, 1999a; Snoeks, 2001). A first extensive report on these taxa appeared in the final report of the SADC/GEF project (Hanssens, 1999b). During the current project, this study was continued by Mark Hanssens. It resulted in the description of 47 species, which makes it one of the most diverse species assemblages in the lake. A dedicated chapter on these fishes will be included in a book to be published soon (Snoeks, in prep).

The rehabilitation of Bathyclarias

This study was undertaken by Lemuel Anseume and Guy Teugels (1999). In 1961, Greenwood synonymised the genera *Bathyclarias* and *Dinotopterus*; the former including 13 species endemic to Lake Malawi, the latter comprising only one species endemic to Lake Tanganyika. This act was questioned in the subsequent literature. In the present study, new morphological and osteological data were combined; their analysis clearly demonstrated that *Bathyclarias* should be rehabilitated as a valid separate genus, endemic to Lake Malawi.

Further results

Other results of work executed during the project, include contributions to the descriptions of *Otopharynx pachycheilus* (Arnegard & Snoeks, 2001), the first deep-water Lake Malawi cichlid with hypertrophied lips, and of a new shallow-water *Lethrinops* (Ngatunga & Snoeks, accepted), and the preparation of a first-ever chapter on the zoogeography of Lake Malawi cichlids, based on literature, the SADC/GEF collections and the data collected during both this and the SADC/GEF project.

All relevant project's results will be integrated in the chapters of a book on the taxonomy, identification and distribution of Lake Malawi cichlids (Snoeks, in prep.).

Large reference collections were left at the Senga Bay station (Malawi) and Kyela (Tanzania) after the closure of the SADC/GEF project, while other parts were sent to the J.L.B. Smith Institute for Ichthyology in Grahamstown (South Africa) and the Africa Museum in Tervuren, Belgium. The latter collection is currently being revised and registered, and in the process of being integrated in FISHBASE. Within the FISHBASE Consortium, the Africa Museum currently assumes the responsibility for African fresh and brackish water fishes.

Problems encountered

No real difficulties were encountered to implement the taxonomic part of the project. The initial drawback of Jos Snoeks not being able to operate from his home institute, the Africa Museum, during the first year, has turned into a major advantage. Through his secondment to the GEF SADC/GEF Lake Malawi/ Nyasa Biodiversity Conservation project, an active and complementary collaboration between the taxonomic parts of the two projects could be achieved, resulting in a beneficial situation for both projects. In addition, he had much more opportunity to assist the team at the lakeside.

Publications and papers

- Anseume, L. & Teugels, G. G. 1999. On the rehabilitation of the clariid catfish genus *Bathyclarias* endemic to the East African rift Lake Malawi. *Journal of Fish Biology* 55: 405-419.
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List of other communications:

- 04 - 05 March 1999 : SADC/GEF Lake Malawi/Nyasa Biodiversity Conservation Project Conference, Senga Bay, Malawi : presentation of a plenary lecture entitled : "Systematics, biodiversity and Lake Malawi/Nyasa fishes";
- 26 November 1999 : The National Museums of Kenya, Nairobi. Presentation of an invited lecture entitled : "The East African cichlid fishes : a unique example of biodiversity within the world of vertebrates."
- 17 December 1999 : University of Innsbruck, Austria, presentation of an invited lecture entitled : "The large East African Lakes : unique centres of fish diversity."
- 19 - 22 July 2000 : International symposium on Great Lakes of the World (GLOW II), Sligo, Ireland; presentation of a lecture entitled : "Systematics of the cichlids of the East African Lakes: from chaos to complexity".
- 3 - 5 Oct. 2000 : Challenges to sustainable development and management of the Lake Malawi/Nyasa Ecosystem" at the World Bank Head Office, Washington; presentation of a lecture entitled : "Systematics and fish diversity of Lake Malawi/Nyasa/Niassa and the challenge to management".
- 30 Oct. – 5 Nov. 2000 : International Symposium on Freshwater Fish Conservation" Montechoro, Portugal; presentation of a lecture entitled : "Lake Malawi/Nyasa fishes and their conservation : a systematist's viewpoint."
- 5 – 10 Jul. 2001 : Annual meeting of the American Society of Ichthyologists and Herpetologists" Penn State, USA; presentation of an invited lecture entitled : "The phylogeny of the East African cichlids: a morphologist's view".
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Conclusions

For their revisions, the taxonomy team has concentrated at the same time on the economically important species and those that were involved in other studies (genetics and life history) such as the *C. virginalis* complex, *P. sp.* 'platyrhynchos', the deep-water *Lethrinops* and *Mylochromis anaphyrmus*.

It has become clear that, though the taxonomy of Malawi cichlid species was already regarded as difficult, still more and unexpected problems keep coming up (Snoeks, 2000, 2001). An obvious case in point is the discovery of more than 40 new species in the sub-flock of the deep-water *Placidochromis*. Clearly as only just over 300 of the estimated 800 or more species are scientifically described, there is still a long way to go.

Also on a higher level, taxonomic problems became acute. Though the classification of the haplochromine taxa has been revised relatively recently (Eccles & Trewavas, 1989), still many problems on the genus level persist or newly emerge as many new taxa are discovered that do not seem to fit the current genus definitions.

Next to the genus and species level issues, during this project for the first time we tried to look at the population level characteristics using morphometric techniques. This resulted in a clear indication that non-mbuna species are not homogeneous in their morphology over their distribution range.

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**Partner 4: University of Hull, Department of Biological Sciences,
Molecular Ecology and Fisheries Genetics Laboratory
(UHULL.DBS.FG)**

Task 4: Fish Taxonomy - Molecular Genetic support

Reporting scientists: Paul W Shaw & Gary R Carvalho

Objectives.

The aim of the Hull-based molecular genetics programme was to explore the phylogenetics and population structuring of Lake Malawi demersal and pelagic cichlids in order to clarify tentative trophic relationships. This was done in close collaboration with the genetics team of RBINS.FBL. The molecular component of the project was undertaken by Dr P W Shaw between 01 April 1999 – 30 November 1999, with the collaboration of externally funded personnel, including Dr L. Hauser (Hull University), Mr M.S.Shekhar (UNESCO-funded) and a PhD student, Mr R Idid (Malaysian Government). The priority activities included the provision of genetic data to all partners for incorporation into appropriate modelson those species selected as dominant and co-dominants in the demersal zone.

Scientific Activity Report

Population structuring of demersal / pelagic species.

DNA was successfully extracted from all available samples of two deepwater demersal species, *Lethrinops albus* and *Placidochromis platyrhynchus*. All samples available from the project (~600 fish) were genotyped at 6 microsatellite loci. In addition, data on the commercially important pelagic species *Diplotaxodon limnothrissa*, collected during an earlier project in our laboratory (DfID-funded “Biodiversity and conservation of Lake Malawi pelagic cichlids”) were reanalysed and incorporated into the present study dataset. Analysis of gene frequencies and estimates of genetic differentiation (F-statistics) were completed on samples collected from several different shelf areas within the Malawian sector for the demersal species (SE Arm, Domira Bay, Nkhotakota, Chinteché) and throughout the lake for *D.limnothrissa* (Table 18), and including samples collected at different locations and depths within areas. No significant genetic differences were observed among any of the samples of *D.limnothrissa*, suggesting that there was no evidence for gross stock structuring or cryptic taxa within this species. Similarly, no evidence was found for substantial genetic differences between samples of *P.platyrhynchus*, although some small but significant differences between samples suggest that levels of gene flow (ie migration) between areas is not extensive. In contrast, significant differences were observed among the samples of *L.albus*, both within and between geographically distinct shelf areas, with by far the most distinct samples coming from the area near Nkhotakota. The results for *L.albus* are consistent with hypotheses of restricted migration between areas and/or the presence of cryptic taxa (species) within samples - further analyses will be needed to confirm or exclude the latter.

Species molecular systematics.

592 base pair DNA sequences from 50 individuals assigned to 18 species of *Lethrinops* and *Taeniolethrinops* were aligned and analysed for phylogenetic relationships. As found by several recent studies of lake Malawi cichlids, genetic divergence between species of these genera is not great enough to allow unambiguous associations within and between species to be discerned. However, a major division between two groups of species, one containing all *Taeniolethrinops* species studied plus *L.albus*, *L.marginatus*, *L.auritus* and *L.cf fucifer*, the other containing all other *Lethrinops* species studied, was identified. Inclusion of these species within a tree of the wider Lake Malawi haplochromine flock indicates that the first group lies within the so-called “non-mbuna” or “demersal” clade, and that the second group lies within the so-called “mbuna” clade. No statistically supported associations could be identified between species within the groups, or confirmation of individuals to their putative species.

Population structuring and phylogenetic analyses of Lake Malawi demersal / pelagic cichlids

Two different molecular approaches were carried out to address different aspects of the genetics part of Task 4:

1. Assessment of population sub-structuring within selected target species, using microsatellite DNA allele frequency data.
2. Phylogenetic reconstruction of relationships among individuals of the *Lethrinops* and *Taeniolethrinops* genera, using direct sequencing of the mitochondrial DNA (mtDNA) Control Region (CR).

Owing to the very high levels of polymorphism observed at all loci (mean number of alleles per locus = 39), it was decided to use four loci (Pzeb1, Pzeb2, Pzeb3 and Pzeb4) screened in a previous study of Lake Malawi rocky shore “mbuna” cichlids (van Oppen *et al.* 1997b) for comparative purposes, plus two loci (UNH130 and UNH154 - Lee & Kocher 1996) showing most consistent amplification and least indication of “null” alleles. It was also decided to use sample sizes of at least 50 individuals where possible to achieve suitable levels of accuracy in allele frequency estimates. Ten samples, representing several different shelf areas within the Malawian sector for the demersal species (SE Arm, Domira Bay, Nkhotakota, Chintechi), and including samples collected at different locations and depths within areas, were screened (Table 18; Figs. 6 and 7 for details and locations). In addition, data from five samples of *D.limnothrissa* (Table 18 and Fig. 6), collected during an earlier project in our laboratory (DfID “Biodiversity and conservation of Lake Malawi pelagic cichlids”) were reanalysed and incorporated into the present dataset. These three species were used as representative of demersal and pelagic cichlids with wide geographical distribution and high abundance, and consequently of importance to potential fisheries. No data are available for potential temporal structuring within the pelagic cichlid populations, due to the problems encountered with repeat trawl surveys.

Total DNA was extracted from ethanol-preserved fin clips using a salting-out method modified from Bruford *et al.* (1992). Genotypes of each individual at each locus were

revealed by PCR amplification of 1/100 dilutions of total DNA with locus-specific primers, one of which is labelled with fluorescent dye, using the following protocol: 2 min. @ 93 °C, followed by 35 cycles of 30s @ 91 °C, 45s @ 55 °C, 10s @ 72 °C. PCR products were run out on an ALFexpressTM automated sequencer and relative mobilities (in base pairs) of alleles scored against internal size standards with Fragment ManagerTM software (Pharmacia Biotech). Standard individuals were used on all gels as controls between runs, as well as the calibrated internal size markers, to ensure homologous allele scoring across the large number of runs scored. Standard population genetic analyses were performed to check all samples for evidence of linkage between loci or departure from random (outcrossing) genotypic expectations. Tests for significant genetic heterogeneity between samples were performed using Exact Tests of allele / genotype frequencies, and via the departure of a measure of genetic differentiation (Fst) from zero, using Genepop (Raymond & Rousset 1995) and FSTAT (Goudet 1995) analysis packages.

Table 18: Locations and number of individuals screened at 6 microsatellite loci for demersal / pelagic cichlid population samples (see Figs. 1 & 2 for further information on locations)

Sample name	Location	Sample size screened
<i>L.albus</i> “deep”		
LSEA1	SE Arm - 125m	47
LSEA2	SE Arm - 100m	43
LSDOM1	South Domira Bay - 100m	50
LSDOM2	South Domira Bay - 125m	50
LDOM	Domira Bay - 125m	40
LNKHOT	Nkhotakota - 100m	64
LCHIN	Chinteché - 125m	51
<i>P.platyrrhynchus</i>		
PSEA	SE Arm - 125m	46
PDOM	Domira Bay - 125m	86
PNKHOT	Nkhotakota - 100m	54
<i>D.limnothrissa</i>		
DN1	inshore - North	93
DN2	offshore - North (35m)	95
DN3	offshore - North (45-53m)	97
DS1	inshore - South - unexploited	95
DS2	offshore - SE Arm - exploited	95

Phylogenetic reconstruction of *Lethrinops* and *Taeniolethrinops*

Mitochondrial (mt)DNA sequencing

Fifty individuals assigned to 18 species of *Lethrinops* and *Taeniolethrinops* were used in the DNA sequence analysis. The list of species used is given in the legend to Fig.9. Total DNA was extracted from ethanol-preserved fin clips using a salting-out method modified from Bruford *et al.* (1992). An initial round of PCR amplification of the target region was conducted to produce template DNA suitable for sequencing. Template DNA was isolated from the PCR mix using Quiagen PCR-Cleanup kits. Approximately 200ng of template DNA was then used in a cycle-sequencing procedure employing fluorescently labelled sequencing primers - the products of these reactions were run out and scored on an ALFexpressTM (Pharmacia Biotech) automated sequencer. Primers and protocols used for the Control Region (CR): initial amplifications used primers FISH L15926 (5'-gAgCgCCggTCTTgTAAKCC - modified from L15926 of Kocher *et al.* 1989) and H00650 (5'-TgATAgTAAAgTCAggACCAAgC - modified from H00651 of Kocher *et al.* 1989) in a protocol of 3 min at 94°C followed by 35 cycles of 30s at 93°C, 45s at 65°C and 30s at 72°C. These primers amplify a product approximately 1.1Kb in length, encompassing the entire Control Region, and which can subsequently be used as a specific template for all sequencing primers. Sequencing reactions used primers THR2 (5'-CCCCTAACTCCCAAAGCTAg - modified from THR of Kocher *et al.* 1993) and L16500 (5'-ATTATTCCTggCATCTggTTCC) for "light" strand sequencing and primers H00650 (as above) and TDKD (Kocher *et al.* 1993) for the complimentary "heavy" strand sequencing, in separate reactions in a protocol of 2 min at 93°C, followed by 20 cycles of 15s at 91°C, 30s at 65°C and 45s at 72°C.

All sequence profiles for a particular region from an individual were aligned within the ALFWINTM sequencing package, a consensus produced and exported for further analysis. All individual consensus sequences were aligned using the ESEE (Cabot and Beckenbach, 1989) sequence editor, and the minimum number of insertions (gaps) added to allow complete alignment of sequences. Estimates of genetic similarity between sequences were made using a range of distance measures, which make different assumptions / adjustments for mutational history of the DNA region: simple pairwise differences; Jukes-Cantor distance; Kimura 2-parameter distance. Distance matrices were then subjected to a Neighbour-Joining algorithm to construct phylogenetic trees, with bootstrap resampling (1000 replications) methods used to assess relative support for the branching patterns, and therefore individual groupings revealed. Phylogenetic relationships among sequences were also assessed, displayed and tested using Maximum Parsimony and Maximum Likelihood methods. All analyses were performed within the PAUP* 4.0 (Swofford 1998) phylogenetic analysis package.

Results Achieved

Genetic variability in Lake Malawi demersal and pelagic cichlids.

All six microsatellite loci screened exhibited high levels of variation across the three species sampled, with number of alleles per locus ranging from 25 in Pzeb3 to 59 in Pzeb1, and expected heterozygosity (“gene diversity”) ranging from 0.73 at Pzeb3 to 0.96 at Pzeb1, Pzeb2, Unh130 and Unh154 (in at least one species). No evidence of linkage disequilibrium was found between any of the six loci, confirming that they can be considered as independent genetic markers.

Levels of genetic variability were distinctly different among the three species, *L.albus* “deep” displaying higher and *P.platyrrhynchus* lower values than *D.limnothrissa* - global estimates (all samples combined, n = individuals genotyped) of number of alleles (A), observed heterozygosity (Ho) and expected heterozygosity (He):

<i>L.albus</i> “deep”	n = 340	A = 40.5	Ho = 0.84	He = 0.92
<i>P.platyrrhynchus</i>	n = 186	A = 25.2	Ho = 0.69	He = 0.75
<i>D.limnothrissa</i>	n = 479	A = 37.7	Ho = 0.78	He = 0.88
<i>(D.macrops</i>	n = 234	A = 32.3	Ho = 0.79	He = 0.87)
<i>(D.”offshore”</i>	n = 234	A = 34.7	Ho = 0.79	He = 0.89)

Some effect of sample size may affect values for *P.platyrrhynchus*, but this is unlikely to wholly explain the difference as values were found to be consistent among the pelagic species examined in a previous study (DfID “Biodiversity and conservation of Lake Malawi pelagic cichlids”) irrespective of total sample sizes (see values for *D.macrops* and D”offshore” above).

Levels of observed heterozygosity are substantially, and significantly, lower than expected heterozygosity in all three species. This is due to significant departures from outcrossing predictions for genotype proportions, exclusively deficits of heterozygotes. It is presumed that these deficits result from the presence of non-amplifying “null” alleles, as demonstrated to be common in other Lake Malawi cichlids by van Oppen *et al.* (1998) – the presence of null alleles does not affect the ability of the heterogeneity tests to detect differentiation between samples.

1.2 Geographical population genetic differentiation within demersal / pelagic cichlids.

Exact tests of allele frequencies (Table 19) and estimates of genetic differences (F_{ST} – Table 20) over all samples indicate that there is no substantial genetic sub-structuring within populations of *P.platyrrhynchus* or *D.limnothrissa*, but that there is highly significant genetic differentiation within the *L.albus* “deep” population:

Table 19: Exact test probabilities of allele frequency homogeneity, at 6 microsatellite loci and over all loci combined, among samples of the three target cichlid species.

Locus	Pzeb1	Pzeb2	Pzeb3	Pzeb4	Unh130	Unh154	Combined
Species							
<i>L.albus</i> “deep”	<0.001	0.187	0.240	<0.001	0.053	<0.001	<<0.001
<i>P.platyrhynchus</i>	0.122	0.155	0.218	0.454	0.216	0.900	0.191
<i>D.limnothrissa</i>	0.087	0.057	0.407	0.144	0.410	0.001	0.002

Table 20: F_{ST} (genetic differentiation) values, at 6 microsatellite loci and over all loci combined (P = probability of overall F_{ST} not > 0, significant locus F_{ST} values are denoted with asterix), among samples of the three target cichlid species.

Locus	Pzeb1	Pzeb2	Pzeb3	Pzeb4	Unh130	Unh154	Overall	P
Species								
<i>L.albus</i> “deep”	<u>0.006</u>	0.001	<u>0.005</u>	<u>0.036</u>	<u>0.002</u>	<u>0.005</u>	0.009	<0.001
<i>P.platyrhynchus</i>	<u>0.006</u>	0.000	<u>0.014</u>	0.000	0.003	<u>0.000</u>	0.003	0.040
<i>D.limnothrissa</i>	0.001	0.001	0.002	0.001	0.000	<u>0.002</u>	0.001	0.017

Lethrinops albus “deep”

Over all loci, both Exact Tests (Table 2, $P = << 0.001$) and F_{ST} estimates (Table 20, $F_{ST} = 0.009$, P that F_{ST} not > 0 is < 0.001) indicate there to be highly significant differences among samples from the four shelf areas screened. Single locus tests show this genetic differentiation to be spread over multiple loci (3-5 loci out of 6). Pairwise multi-locus Exact tests show that all samples have significantly different allele frequencies. Pairwise multi-locus F_{ST} values indicate that levels of differentiation among the samples are not uniform: the sample from Nkhotakota exhibits values at least double those seen among the other samples. After the Nkhotakota sample, the SE Arm sample appears to be responsible for much of the significant differentiation, with the Domira Bay and Chinteché samples showing small, marginally significant, levels of differentiation among them.

Table 21: Pairwise F_{ST} values (below diagonal, * = $P < 0.05$, ** = $P < 0.01$ *** = $P < 0.001$ that F_{ST} not > 0) and Exact test probabilities of allele frequency homogeneity (above diagonal), over all 6 microsatellite loci combined, for samples of *L.albus* “deep”. Values in bold are ones remaining significant at $P < 0.05$ after Bonferroni correction for multiple tests.

	LSEA	LSDOM	LDOM	LNKHOT	LCHIN
LSEA		0.0059	0.0358	<0.0001	<0.0001
LSDOM	0.0029 **		0.0036	0.0002	0.0023
LDOM	0.0014	0.0032*		<0.0001	0.0023
LNKHOT	0.0192 ***	0.0108 ***	0.0207 ***		<0.0001
LCHIN	0.0065 ***	0.0032*	0.0033**	0.0161 ***	

Although highly significant, according to departures of F_{ST} from zero, the level of genetic differentiation seen among *L.albus* “deep” samples (overall $F_{ST} = 0.009$, range 0.0014-0.0207) is relatively low compared with that recorded for other Malawi cichlid species displaying distinct population sub-structuring, especially in view of the difference in geographical scale over which the samples were collected (over a range from ~50-250 km in this study): overall $F_{ST} = 0.151$ over 0.9 - 42.4 km in *Melanochromis auratus*, Markert *et al.* (1999); overall $F_{ST} = 0.079$ over 0.6 - 10.4 km in *Labeotropheus fuelleboni*, Arnegard *et al.* (1999); $F_{ST} = 0.007$ - 0.016 over 3 km in 4 species of the *Pseudotropheus* complex, van Oppen *et al.* (1997b). Levels of between-area differentiation in *L.albus* “deep” are, however much higher than observed for the “unstructured” pelagic species (see *D.limnothrissa* below), so it must be concluded that the population of this species within the Malawi sector of the lake is significantly sub-structured, and that levels of gene flow (migration) between areas are likely to be small. One possible complicating factor to add to this conclusion is indicated by the differences between samples collected within the SE Arm and southern Domira Bay (Fig.7 - SEA1 & 2, SDOM1 & 2): samples collected at different depths show distinctly different allele frequency profiles at locus Pzeb4. Over all loci, exact tests and F_{ST} tests show that SEA1 and SEA2 are significantly different ($F_{ST} = 0.0044$, $P = 0.02$), whereas SDOM 1 and SDOM2 are not significantly differentiated overall ($F_{ST} = 0.0017$, $P > 0.05$). One explanation for this result is that there are genetically differentiated demes mixed together, either within samples or between samples at different depths: this could indicate cryptic species within *L.albus* “deep” as it is currently recognised. Mixes of several species could produce the pattern of genetic differences. But whatever the underlying explanation, it is clear that the population of *L.albus* “deep” as it is currently recognised shows significant genetic sub-structuring both between and within different shelf areas of Lake Malawi.

Placidochromis platyrhynchus

Over all loci, both Exact Tests (Table 19, $P = 0.191$) and F_{ST} estimates (Table 20, $F_{ST} = 0.003$, P that F_{ST} not $> 0 = 0.04$) indicate there to be no substantial differences among samples from the three areas screened. Pairwise tests (Table 22) also confirm a lack of marked genetic differentiation among the samples, although F_{ST} estimates between the Domira Bay sample and the other two areas are just significantly greater than zero (not significant if P adjusted for multiple tests)

Table 22: Pairwise F_{ST} values (below diagonal, * = $P < 0.05$ that F_{ST} not > 0) and Exact test probabilities of allele frequency homogeneity (above diagonal), over all 6 microsatellite loci combined, for samples of *P.platyrrhynchus*. Values in bold are ones remaining significant at $P < 0.05$ after Bonferroni correction for multiple tests.

	PSEA	PDOM	PNKHOT
PSEA		0.0561	0.1592
PDOM	0.0031*		0.2712
PNKHOT	0.0009	0.0036*	

Diplotaxodon limnothrissa.

Over all loci, both Exact Tests (Table 19, $P = 0.0014$) and F_{ST} estimates (Table 20, $F_{ST} = 0.0012$, P that F_{ST} not $> 0 = 0.017$) indicate statistically significant differences among the five samples screened. There is however, little evidence of substantial and systematic genetic differences among samples indicating population sub-structuring. The Exact Test is extremely conservative, and examination of single locus results indicates the overall value to be due largely to one locus (Table 19 - Unh154) only. The overall F_{ST} value is also exceedingly small in comparison to values observed in other Malawi cichlid species (see examples cited above), especially in view of the difference in geographical scale over which the samples were collected (over a range of 460 km for this species). Finally, examination of pairwise Exact Tests and F_{ST} values between samples (Table 23) shows only a single significant difference (Exact Test between D.lim14 and D.lim38) after Bonferroni correction of probabilities for multiple tests, and no obvious systematic pattern of genetic differences between samples based on such divisions as northern vs. southern, inshore vs. offshore, or exploited vs. unexploited populations.

Table 23: Pairwise F_{ST} values (below diagonal, * = $P < 0.05$ that F_{ST} not > 0) and Exact test probabilities of allele frequency homogeneity (above diagonal), over all 6 microsatellite loci combined, for samples of *D.limnothrissa*. Values in bold are ones remaining significant at $P < 0.05$ after Bonferroni correction for multiple tests.

	DN1	DN2	DN3	DS1	DS2
DN1		0.0092	0.0900	0.0115	0.0016
DN2	0.0015		0.3168	0.3267	0.0779
DN3	0.0020	0.0005		0.4578	0.0156
DS1	0.0013	0.0009	0.0012		0.0284
DS2	0.0005	0.0009	0.0026*	0.0009	

Conclusion

An illustration of the differing levels of genetic differentiation among samples from the three species examined is given in Fig.6 (for *P.platyrrhynchus* and *D.limnothrissa*) and Fig.7 (for *L.albus* “deep”), which display sample allele frequency profiles at locus Pzeb4 in all samples screened. Locus Pzeb4 has been found to be a sensitive indicator of population sub-structuring, where present, in other Malawi cichlid species (van Oppen *et al.* 1997; P.W.Shaw, unpublished data), and indeed displays distinctly species-specific frequency profiles among the three species examined in this study. From Fig.6 it is clear that within *P.platyrrhynchus* and *D.limnothrissa* all samples exhibit remarkable conformity in allele composition and frequency, throughout the geographical range sampled.

As the range sampled comprises the whole lake for *D.limnothrissa*, and a 200km sector of the Malawian shore of the lake for *P.platyrrhynchus*, it can be concluded that both species comprise single, genetically unstructured populations within Lake Malawi. Higher levels of F_{st} in *P.platyrrhynchus* suggest that migration between areas is probably less than for *D.limnothrissa*: this may mean that although levels of gene flow are high enough to effectively homogenise populations occupying the different shelf areas, levels of migration may not be high enough to quickly restock an area if the resident population crashes.

In contrast, Fig.7 illustrates the distinct differences in allele frequencies among the different areas sampled for *L.albus* “deep”, particularly regarding the relative frequencies of alleles 111, 119, 121 and 123. As discussed above this indicates substantial genetic sub-structuring of the population of this species across geographically separate shelf areas, and suggests limited migration between areas. A suggestion of significant sub-structuring within areas is also apparent from the differences in allele frequencies at locus Pzeb4 observed between samples SEA1 & 2 and SDOM1 & 2 (Fig.7). Whether this is due to genetic sub-structuring of the population by depth, by shoal integrity (related individuals shoal together), or by the presence of several cryptic species within *L.albus* “deep” within these areas will need further study to resolve.

Phylogenetic reconstruction of *Lethrinops* and *Taeniolethrinops*

Fig.8 presents a N-J tree of all *Lethrinops* and *Taeniolethrinops* individuals submitted to the final analysis. The main conclusions to be drawn from this analysis, based on the support attached to branches by bootstrap replication, are:

There are two, possibly three, statistically well-supported groups within the tree. One group contains all individuals assigned to *Taeniolethrinops* species, plus *L.albus*, *L.marginatus*, and *L.auritus*. A small subgroup of the first group (Fig.9) contains the two individuals of *L.cf fucifer* studied. The second main group contains all individuals of the other *Lethrinops* species studied. Inclusion of these species within a tree of the wider Lake Malawi haplochromine flock indicates that the first group lies within the so-called “non-mbuna” or “demersal” clade, and that the second group lies within the so-called “mbuna” clade.

The well-supported branches on the tree contain individuals from multiple species, and within these branches there is no statistical support for, and in fact no real pattern

to suggest that individuals fall out into morphologically defined groups (i.e. species). No statistical manipulation of the sequences or analyses can force all members of each putative species onto well-supported branches. For example, three individuals of *L.longipinnis* “orange head” form a well-supported group, but other individuals assigned to the same species fall elsewhere amongst individuals of other species. Therefore within major groups (clades), the DNA sequence data cannot confirm or refute morphological classifications. Only where individuals of a putative species fall into different groups can the sequence data add to the classification: for example, in separating the members of *L.albus* from *L.cf albus*, and of *L.furcifer* from *L.cf furcifer*.

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Fig. 6: Gene frequencies at locus Pzeb4 for *P.platyrrhynchus* and *D.limnothrissa*

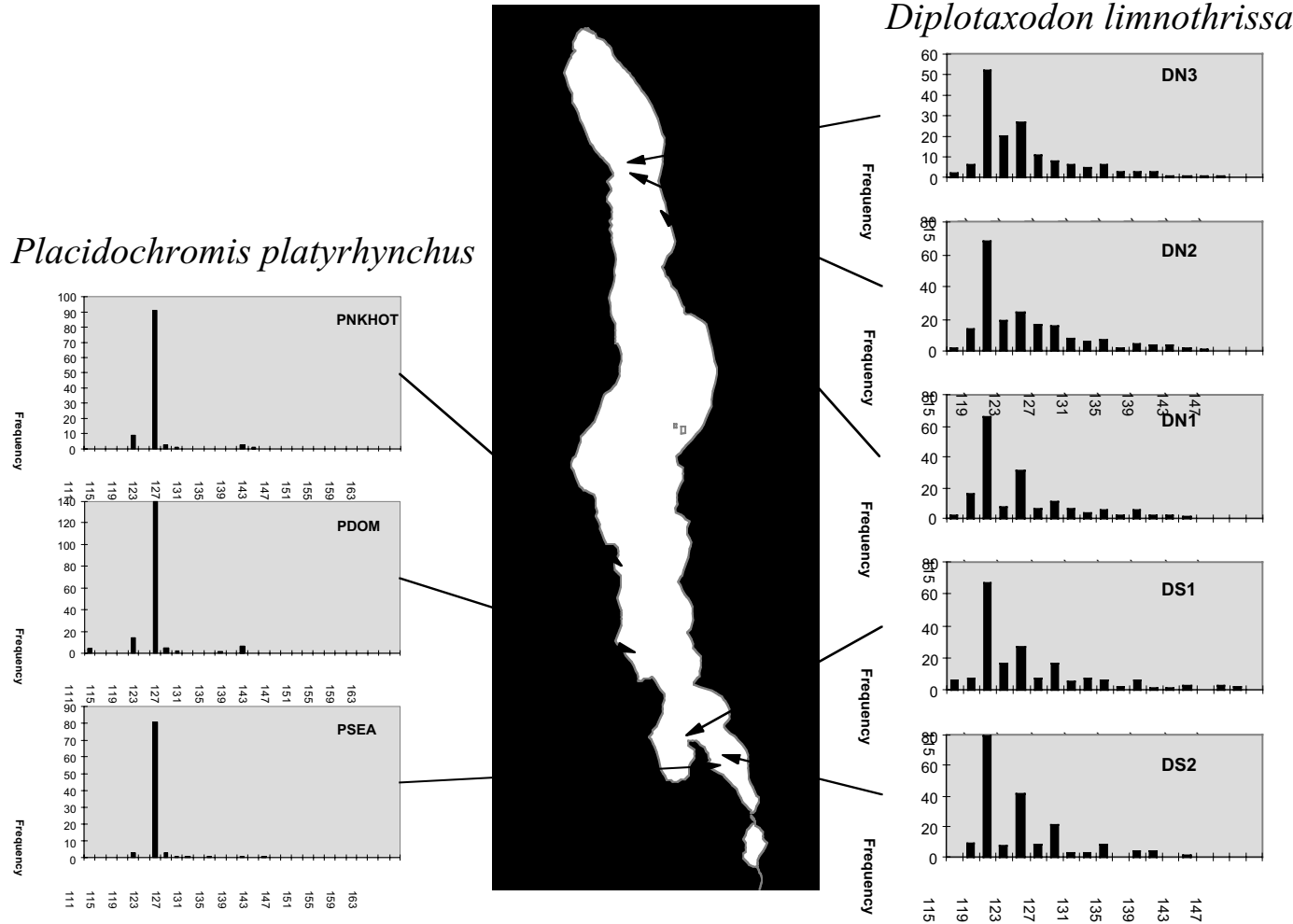


Fig. 7 : Gene frequencies at locus Pzeb4 in *Lethrinops albus* "deep"

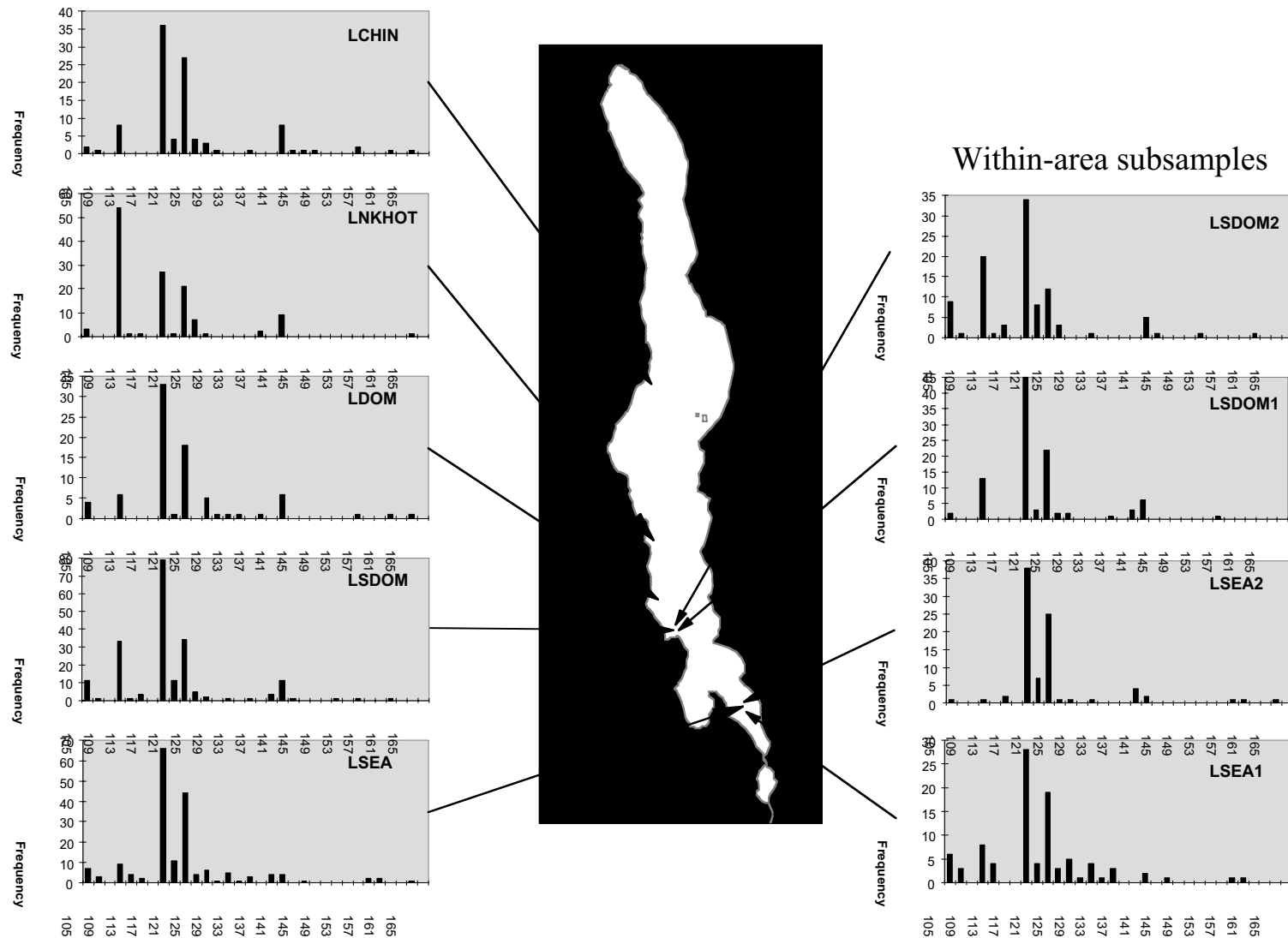


Fig. 8: N-J tree of DNA sequence divergence (K2 distance) between individuals of various species of the *Lethrinops* and *Taeniolethrinops* genera, rooted with two *Rhamphochromis* species.. Figures above branches are bootstrap support (1000reps). Key to species: L.OLIV - *Lethrinops* ‘oliveri’; L.MICRO - *Lethrinops microdon*; L.GOSS- *Lethrinops gossei*; L.LPIN - *Lethrinops longipinnis*; L.FUR - *Lethrinops furcifer*; L.cf FUR - *Lethrinops* cf. “furcifer”; L.ALBUS - *Lethrinops albus*; L.cf ALBUS - *Lethrinops* cf albus; L.MARG - *Lethrinops marginatus*; L.AUR - *Lethrinops auritus*; L.ALTUS - *Lethrinops altus*; L.PARV - *Lethrinops parvidens*; L.LONGOH - *Lethrinops* “longipinnis orange head”; L.LNG - *Lethrinops longimanus*; L.POLL - *Lethrinops polli*; T.LAT - *Taeniolethrinops laticeps*; T.PRE - *Taeniolethrinops praeorbitalis*; T.FURCD - *Taeniolethrinops furcicauda*.

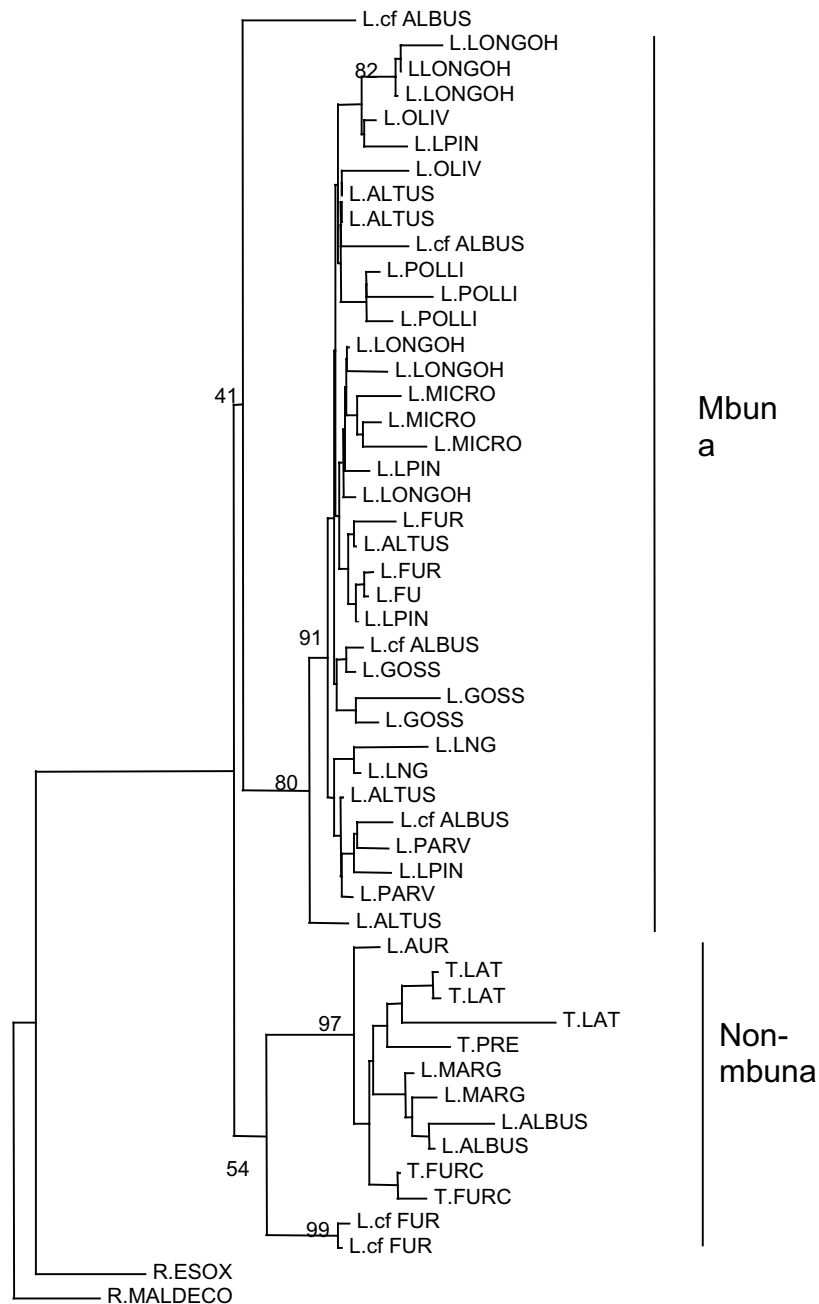
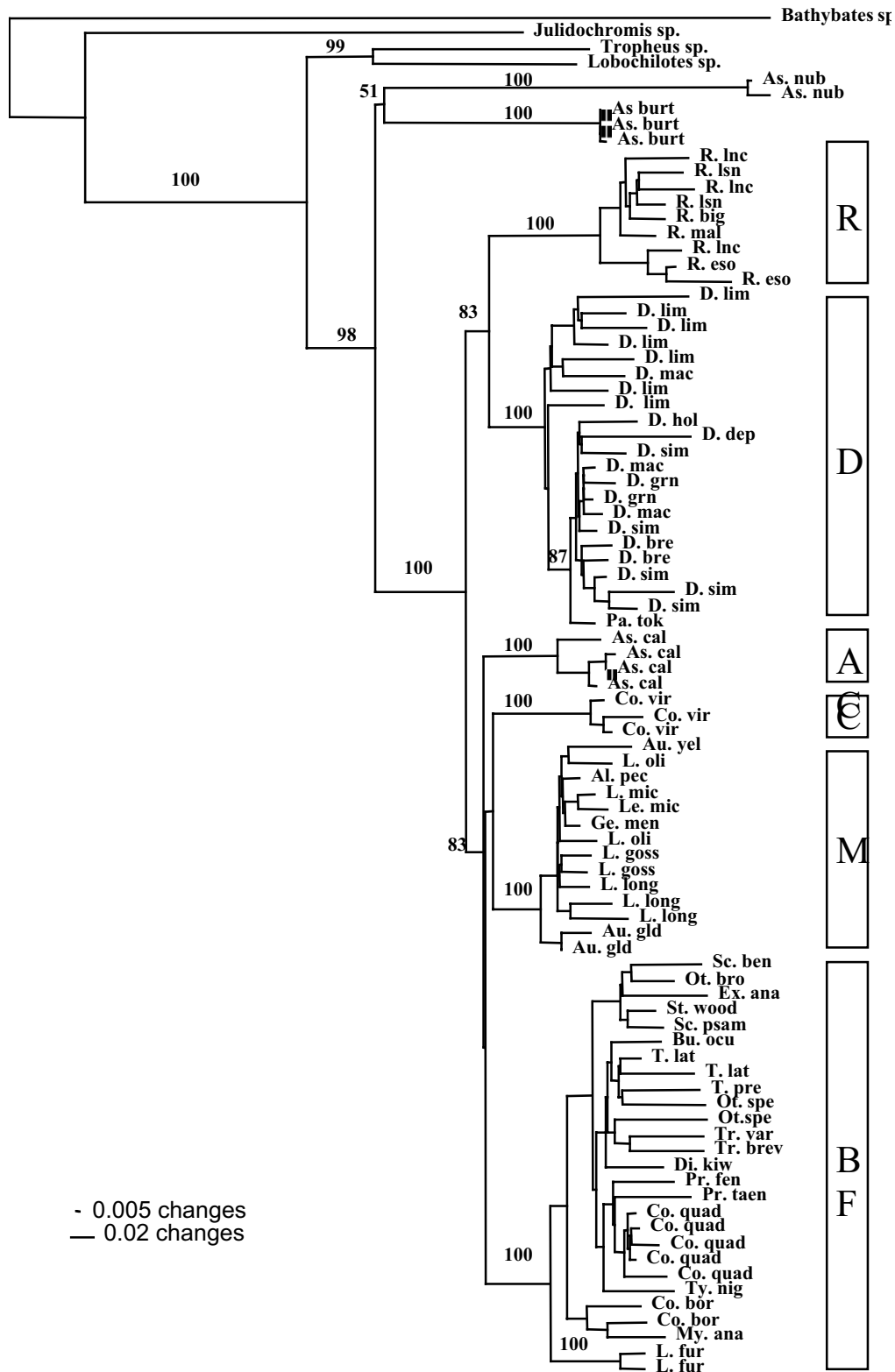


Fig. 9: N-J tree of DNA sequence differences (K2 distance) between members of the major clades of the Lake Malawi haplochromine flock, rooted with species from Lake Tanganyika and Lake Victoria.



Partner 5: University of East Anglia, Overseas Development Group (UEANG.ODG)

Reporting Scientist: E. H. Allison

Other contributors: W. Darwall

Objectives

Fisheries management increasingly adopts an ecosystem-based approach. The goal of this section of the project was to improve knowledge about the structure and function of Lake Malawi's ecosystem, so that policy and management actions addressing the dual concerns of biodiversity conservation and optimisation of fish yields could be based on synthesis of this knowledge.

The specific objectives of this component of the study were therefore:

- 1) A study of the species composition, distribution and relative abundance of fish: Task 5 (with Partners 4, 6, 8, 9 and 10)
- 2) A study of the trophic structure of the Lake Malawi ecosystem, conducted through both stomach contents analysis and stable isotope analysis: Tasks 6 & 7.
- 3) Parameterisation of a trophic model (ECOPATH) to provide a structured, quantitative description of Lake Malawi's benthic ecosystem, to be linked to previous studies of the pelagic ecosystem (Allison et al., 1995): Task 8, with inputs from Tasks 1-5 and all project partners)
- 4) Preliminary use of the ECOPATH model (Christensen et al, 2000) in simulations of different management scenarios and their likely impact on the structure and productivity of the system (ECOSIM scenarios): Tasks 8 and 9

Species losses have already been documented in the most heavily trawled southern arms of Lake Malawi (Turner 1977a; Turner 1977b; Turner *et al.* 1995) yet our knowledge of the tropho-dynamics of this fish community remains insufficient to evaluate how such losses might effect system stability. We don't yet know if there are ecologically equivalent species to buffer species losses within the demersal fish community. With plans for further expansion of the fishery into new habitats we need to increase our basic understanding of the trophodynamics of the system if we are to better predict and manage the impacts of new fisheries. This component of the project aimed to provide some of the tools to make such an assessment.

Scientific Activity Report

The species composition, relative abundance, growth, mortality and diet composition of fish from ten sample stations around Lake Malawi/Niassa were sampled over three research cruises with the R/V Usipa. A total of 356 trawl hauls were made. These trawl samples provided the data for diet composition, stable isotope analysis studies, and other work to parameterise the ECOPATH model (the methods for which are described in other partner reports).

1. Determination of trophic structure and level Diet compositions were determined, from a sample of 2738 stomachs, for 109 species or species complexes which include the species making up between 80-90% of trawl-caught biomass and approximately 35% of taxa recorded as being present in trawl catches. These diet composition data were used to define 'trophic guilds' – collections of species using similar and distinctive combinations of food categories. Hierarchical agglomerative clustering and ordination methods were used to identify groups of species with common diets. Ten trophic guilds have been identified and fractional trophic levels calculated for all 109 species, based on the methods of Pauly *et al* (2000).

Diet compositions determined from stomach analyses are, however, only representative of the last meal. If, as proposed, many of the species are opportunistic feeders and some show ontogenetic and seasonal diet shifts then the results of stomach analyses may only tell part of the story. An alternative technique which examines stable isotope ratios in fish tissue can provide the temporal and spatial information which may be missing from stomach analyses.

Nitrogen isotope ratios were determined for 34 of the most common fish species found in trawl catches. Trophic levels for these species were estimated from their $\delta^{15}\text{N}$ values on the assumption that $\delta^{15}\text{N}$ levels rise through enrichment by approximately 3.3 ‰ with each successive trophic transfer. An enrichment rate of 3.3 ‰ was taken as giving the best fit to the trophic level estimates obtained from the diet data within the range of 2.0 and 5.0 ‰ which is reported for other studies (Peterson & Fry 1987). The main food sources at the base of the food web are thought likely to include a combination of phytoplankton, epilithic algae and detritus (Duponchelle *et al.* 2000). The mean $\delta^{15}\text{N}$ value for these combined food sources was estimated at 1.0 ‰ on the basis of mean values obtained for phytoplankton (0.34 ‰), and sediment (0.34 - 1.41 ‰) in Lake Malawi (Ramlal, pers. comm.).

2. Calculation of food consumption/biomass (Q/B) ratios. This was achieved, for the major species, by taking samples of fish using trawls hauled every two hours over a series of three 24 hour sampling cycles conducted at different depths. The computer program MAXIMS (Jarre *et al.* 1990) was applied to analysing the periodic changes in weight of stomach contents to obtain estimates of food intake and digestion rates, and hence overall food consumption. For less abundant species, Q/B ratios were estimated using empirical methods based on fish morphology and trophic level (Palomares and Pauly, 1998).

3. Parameterising the ECOPATH model involved post-processing of data collected by this study, and by other partners. The model is restricted to the southern shelf of the lake which stretches from Nkhata Bay south to include the two southern arms of the lake and up to Meponda the west coast. Data on fish and invertebrate community structure were obtained from trawl and grab sampling respectively. Annual statistics for fishery catch yields were contributed by the Malawi Fisheries Research Unit (FRU) at Monkey Bay, and were used to parameterise biomass flows to the fishery. Inputs from the pelagic ecosystem were obtained from the Ecopath model produced by the ODA/SADC Project (Allison *et al.* 1995).

4. Running ECOSIM scenarios Ecosim has been proposed as a tool that can be used for "study of fishery response dynamics in any ecosystem for which there are

sufficient data to construct a simple mass-balance model” (Walters, 1997). In this project, we used the ECOPATH models as a basis for simulations of the impacts of changing fishing practices, particularly further increases in demand for fish and consequent fishery effort, and expansion of commercial trawl fisheries.

Results Achieved

1) Quantitative analysis of fish diets and guild allocation based on diet analysis

The criteria used to define each of 10 trophic guilds are illustrated in Figure 10. An additional guild, Guild 11, was formed to incorporate those shallow water species not often encountered in the demersal trawls which were reported in the literature as feeding on epilithic algae and macrophytes.

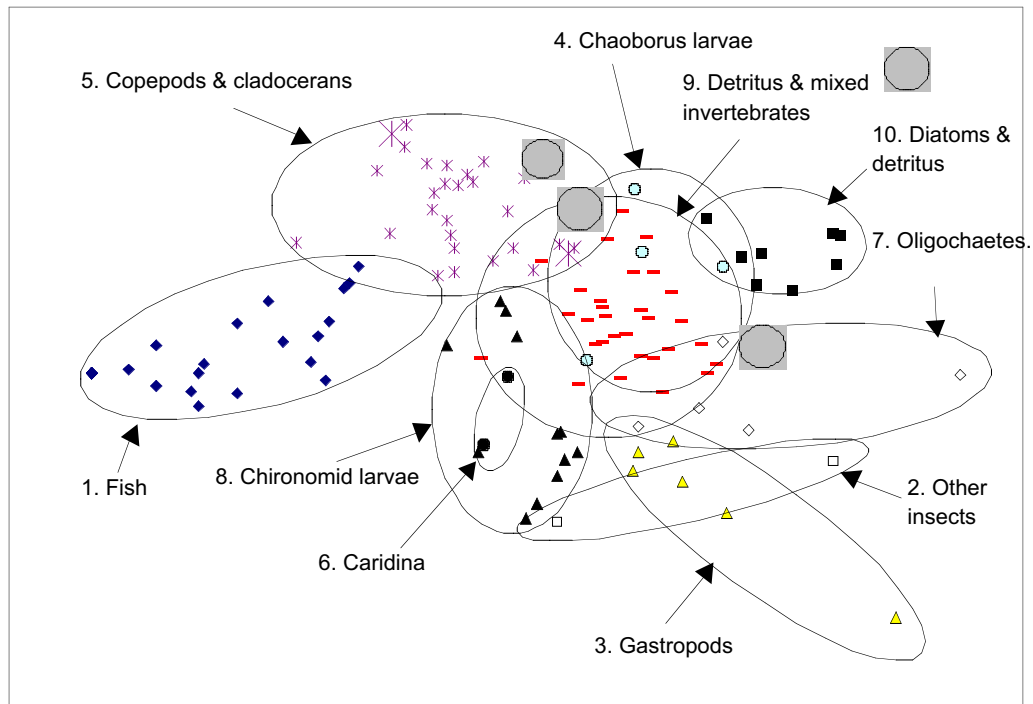


Figure 10. MDS ordination plot showing species scores in multivariate space as defined by Bray-Curtis similarities for diet measures. Species groups are bounded by ellipses as defined by cluster analysis of the trophic guilds and their main dietary items is indicated. Five species which are positioned as outliers from the guilds identified by cluster analysis are enclosed in opaque circles.

2) *Q/B ratios.* Food consumption rates were calculated by fitting consumption-evacuation rate models to data collected on programmes of diel sampling of stomach contents for the dominant species, following the methods outlined in Allison et al., (1996a). An example of fitted consumption-rate models for two important species of *Lethrinops* are given in Figure 11.

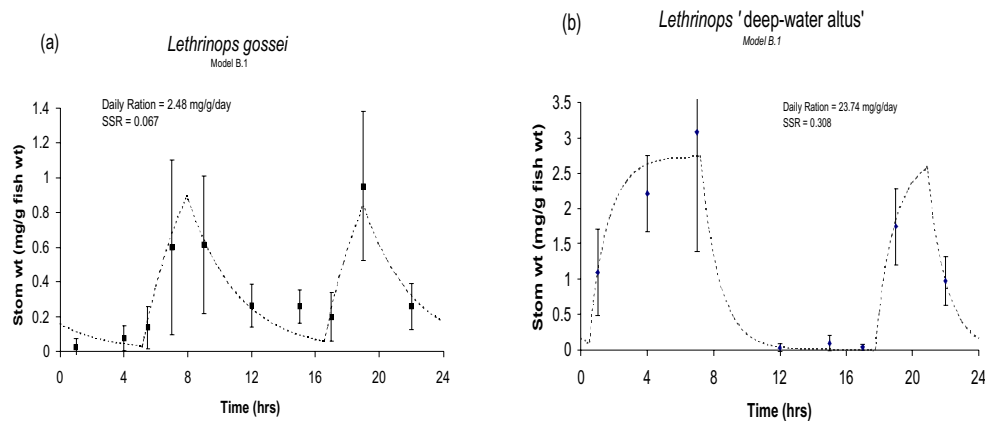


Figure 11. Mean weights, with 95% confidence intervals, of stomach contents (mg) relative to fish body weight (g) of (a) *Lethrinops gosseii*, (b) *Lethrinops 'deep water altus'*, Fitted curves are models of ingestion and evacuation rates (from Sainsbury 1986 and Jarre *et al.* 1991) used for calculation of daily ration.

Calculating food consumption rates from diel stomach contents analysis is difficult and expensive. Most studies rely extensively on use of empirical models linking fish morphometry to consumption/biomass ratios (Palomares and Pauly, 1998). Food consumption rates have been calculated for an additional 35 species using the empirical method.

3) Lake-wide trophic structure. The mean trophic level of the demersal fish community for all depths and sample areas (1998 and 1999 data sets) pooled and weighted by their respective areas of lakebed coverage is 3.18 with the bulk of biomass (58%) concentrated at trophic level 3.0 (Figure 12).

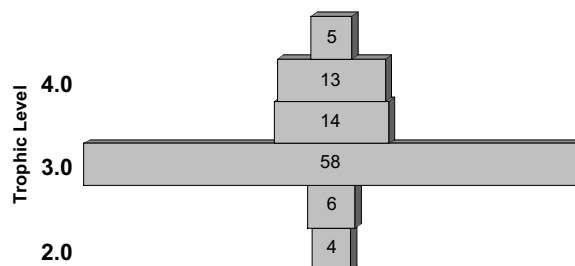


Figure 12. Fish biomass distribution among trophic levels for all areas and depths pooled and weighted by lakebed coverage of sampling. Labels represent the percentage of total biomass in each trophic level, with fractional levels aggregated within 0.5 categories.

Mean trophic values were highly significantly influenced by water depth and sample location (ANOVA, 5 depth bands, 8 locations, 356 samples). The main influence of depth was realised in the shallow water where mean trophic values in the 0-20m depth band were significantly lower than at all other depths (Tukey: $p < 0.001$).

4) Stable isotope analysis. The accuracy of the trophic analysis based on stomach-contents data was tested using stable isotope analysis. The trophic levels calculated from $\delta^{15}\text{N}$ values were compared with those obtained for the same 34 species using

dietary analyses. A Sign test of the difference between estimates from the two methods found no significant difference ($z = -1.281$; $p > 0.05$). On the basis of these findings it is concluded that dietary data from stomach analyses provide a fair representation of the long-term diet compositions of the species examined. A scatterplot further demonstrates the relationship between estimates of trophic level obtained from $\delta^{15}\text{N}$ values and diet analyses (Fig. 13).

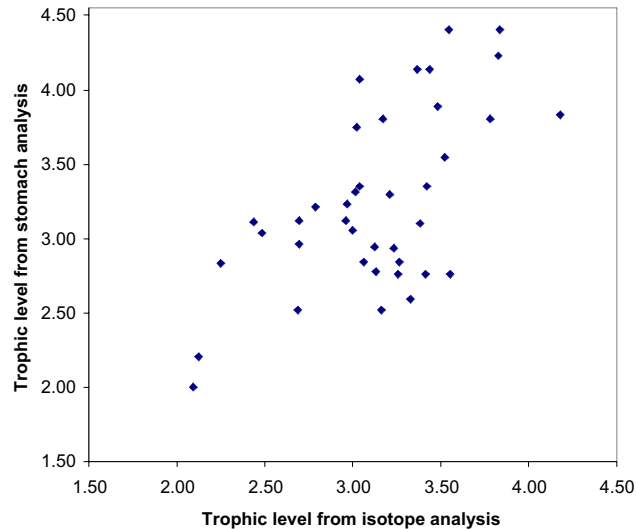


Figure 13. Scatterplot of trophic level values obtained from $\delta^{15}\text{N}$ values (x-axis) and diet analyses (y-axis) for 34 species.

5) Trophic structure, species composition and stability. Use of Multi-dimensional scaling (MDS) plots clearly demonstrate that guild composition is more highly conserved than species composition for those sites which were previously identified as most dissimilar in terms of species compositions (e.g. Fig. 14). As species differentiation between sample areas has not led to significant parallel changes in trophic guild compositions it is concluded that the species replacements are trophic equivalents.

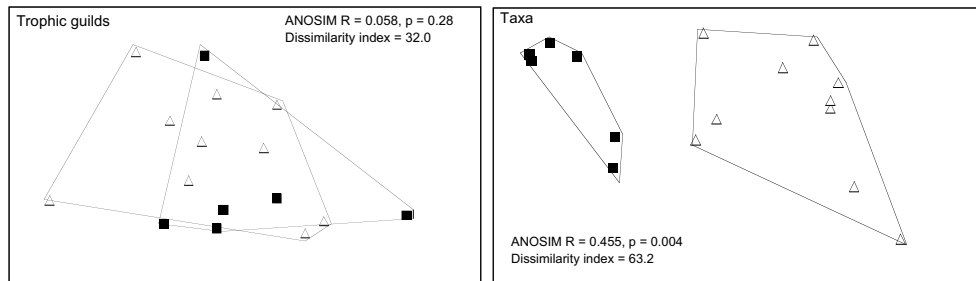


Figure 14. MDS ordination plots demonstrating the relative degrees of taxonomic and trophic guild differentiation between sample areas I (triangles) and VIII (squares) in the 0-20m depth band.

The evidence provided for trophic analogues is sufficient to state that the trophic integrity of the system would be maintained if the species assemblage from any one sample area on the 'southern shelf' was to replace any other within the same depth band. A mean of less than 60% of species shared between sample areas within a 20m

depth band suggests that at least 40% of species within the Lake Malawi demersal fish community are trophic analogues. This allows us to propose a hypothesis of the likely impacts of increased exploitation on the demersal fish community (Figure 15)

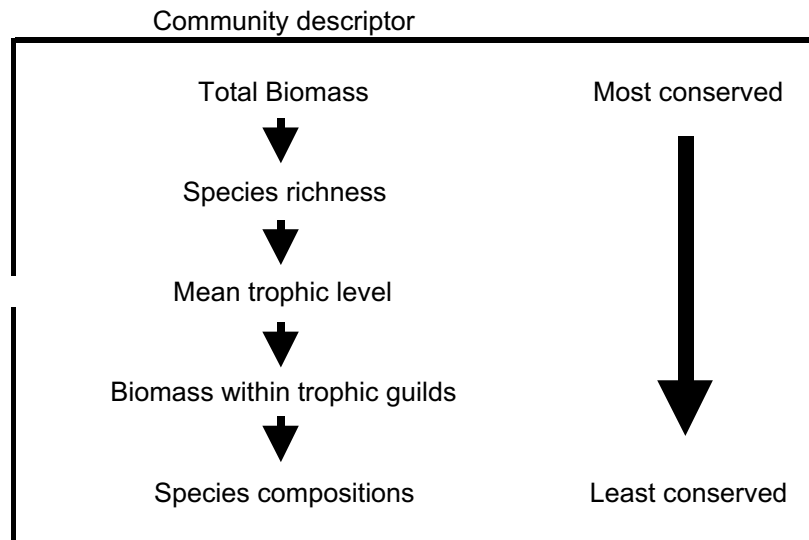


Figure 15. Hierarchical scheme for community assembly, Lake Malawi.

If the ceiling of available energy (resource limitation) is the main limiting factor in community structure one can see how the number of ways in which this might be utilised by increases within each successive level down the hierarchy. For example, species richness would be limited by the number of available niches and the number of adaptations to those niches within the species pool. If, within the species pool a number of species have adaptations to a similar ecological niche then the final assembled community could comprise a number of different species combinations, of functional analogues, such that the spatial variability in species compositions would be high. The total number of species (species richness) would, however, remain conserved as the same number will be required to fill all the available niches. This assumes that resource availability does not change between sample areas.

6) Trophic modelling: Two Ecopath models have previously been developed for the pelagic zone of Lake Malawi (Degnbol 1993; Allison *et al.* 1995) but, until now, despite the many interesting questions on energy flows and benthic-pelagic coupling raised by these earlier studies, there has been no complementary study of biomass flows through the demersal community. One of the main conclusions of the first pelagic model by Degnbol (1993) was that "the pelagic ecosystem of central Lake Malawi produces midge larvae and midges (*Chaoborus edulis*), not fish..". However, the second model (Allison *et al.* 1995) demonstrated that "...*C. edulis* is clearly more important to the fish community than had previously been supposed..." with an estimated 50% of production being consumed by pelagic fish predators. They also suggested that many demersal fish species might be feeding on *C. edulis* larvae that migrate into the sediments on a diel cycle to seek refuge from pelagic predators. As *C. edulis* is a pelagic feeder (Irvine 1997) it was therefore concluded that "...the community of demersal fish is directly tied to pelagic productivity, rather than indirectly through a detrital food chain." (Allison *et al.*, 1996b). Without further information on the demersal food web structure and dynamics the role of *C. edulis*,

the nature of the proposed benthic-pelagic coupling, and the relative importance of pathways supporting the demersal community remained unknown.

A graphical summary of the trophic structure of the combined demersal and pelagic ecosystem is given in Figure 16. Fractional trophic levels are assigned using the weighted average of the trophic level of prey items. The generalised food web spans four trophic levels and has two main bases in detritivory and planktivory. The consumption of detritus is largely by benthic invertebrates although a few fish groups, notably *Oreochromis* spp., specialise in sifting diatoms and other organic matter from the detrital ooze. At trophic level 3 a number of fish groups feed on the benthic invertebrates. Zooplankton is imported into the food web at trophic levels 3 to 4 through fish predation on carnivorous and herbivorous copepods and *C. edulis* larvae. Most fish species are then subject to predation by a large number of piscivorous fish species. The apex predators are *Bagrus meridionalis*, the clariids and some of the large cichlid piscivores that suffer little predation themselves. The only source of primary production within the demersal system itself is macrophytes and algae that are restricted to the shallow water demersal. The longest potential food chain, with six levels, passes from diatoms, through herbivorous copepods, carnivorous copepods, *C. edulis* larvae, fish zooplanktivores, cichlid piscivores, to an apex predator such as *Bagrus meridionalis*.

The euphotic zone in Lake Malawi extends to approximately 50 m depth (Patterson & Kachinjika 1995). Solar penetration to these depths supports photosynthetic activity for the production of the phytoplankton and algae that form the basis of the pelagic and inshore demersal food webs. Organisms living within the euphotic zone can directly exploit these primary producers but those organisms living in deeper water such as in the offshore demersal community will have to rely on the transfer of organic material from the pelagic to the benthic system. The three main transfer mechanisms are; through waste products and dead organisms sinking into the demersal habitat; through demersal species migrating into the pelagic to feed; or active migration of pelagic species into the demersal habitat where they are consumed by demersal predators.

The relative importance of the different pathways of benthic-pelagic coupling to demersal fish production can now be determined from the size of the relevant fluxes (Table 24). Only 2.5% of the biomass consumed at the lowest point of entry into the demersal system is of demersal origin comprising a combination of flows to detritus from fish demersal fish groups and primary production by macrophytes and algae. A "detrital rain" of dying pelagic organisms and faeces accounts for a further 6 % of biomass import. A further 4% of demersal fish biomass is imported as *C. edulis* larvae that are consumed on their migration into or from the sediments. The greatest flow of biomass into the demersal fish is, however, through consumption of copepods (55.5%) and diatoms (33%) from the pelagic ecosystem. Diatoms are most likely consumed from within the sediments having dropped out of the pelagic.

In summary, the demersal system appears to rely most heavily on biomass imported from the pelagic through consumption of copepods by fish migrating vertically to feed in the pelagic, and through a fall out of diatoms which are consumed by fish sifting them from the sediment ooze.

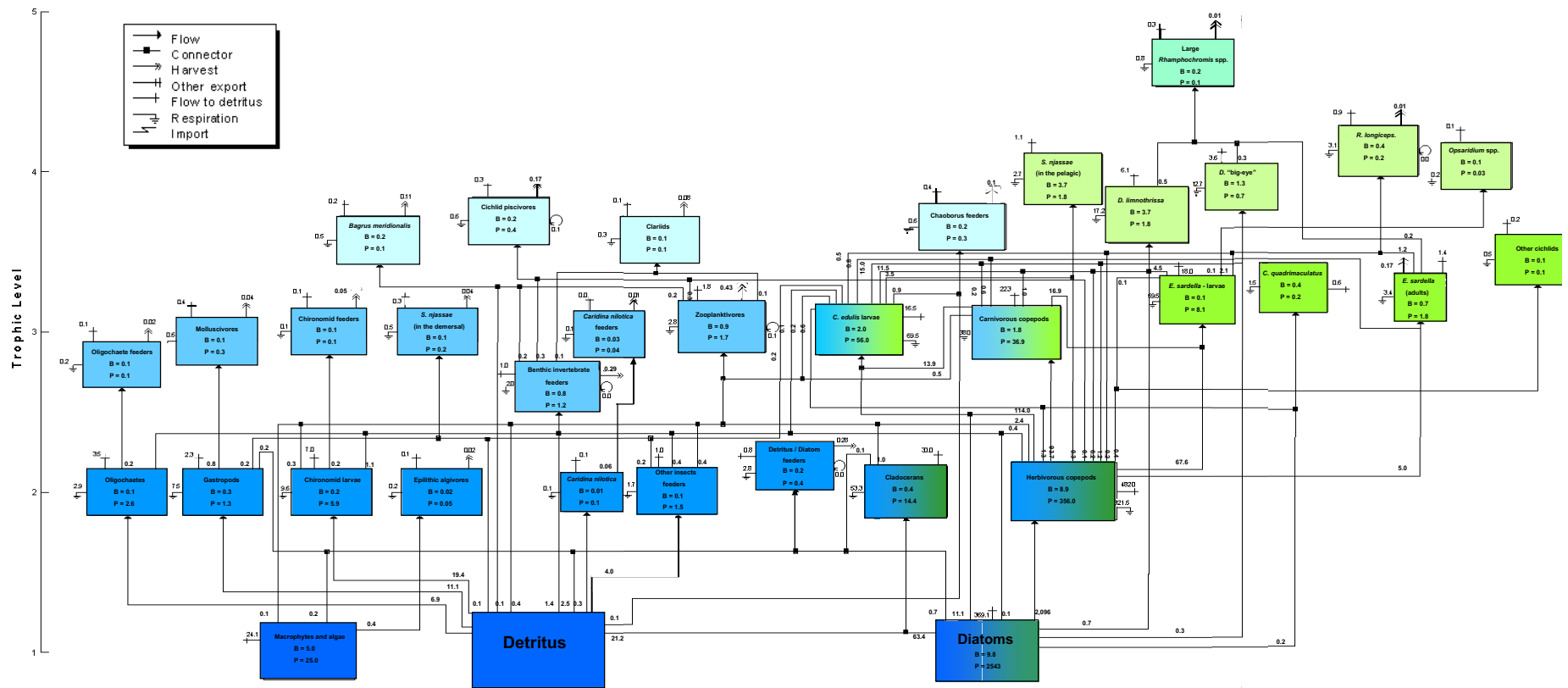


Figure 16. Box model of the Lake Malawi ecosystem. Boxes represent standing biomasses (B , g m^{-2}); the area of each box is proportional to the log of biomass. Production (P) is in $\text{g m}^{-2} \text{year}^{-1}$. Blue coloured boxes represent groups that are within the demersal system and green coloured boxes represent groups within the pelagic system. Two-tone blue/green coloured boxes represent groups within the pelagic system which have significant flows into the demersal system. Flows between boxes represent consumption (Q $\text{g m}^{-2} \text{year}^{-1}$). Flows of $<0.1 \text{ g m}^{-2} \text{year}^{-1}$ are omitted for clarity. Flows entering the lower half of each box are consumption, those leaving the top are predatory losses, respiration, flow to detritus and yield to fisheries. Lines of flow merge at junctions, but do not branch.

Table 24. Sources of biomass import to the demersal ecosystem.

Ecosystem Component	Origin	t/km/year consumed	% total
Detritus	Pelagic	63.5	6.0
Detritus	Demersal	4.3	0.5
Copepods	Pelagic	627.8	55.5
Chaoborus larvae	Pelagic	46.6	4.0
Diatoms	Pelagic	371.7	33.0
Macrophytes/algae	Demersal	24.1	2.0
Total	Combined	1138.0	100

The mean trophic level of harvested fish is 2.99 and shows the fisheries to be harvesting from relatively high in the food-web. The catch yields for each trophic level are summarised in Table 25. It has been demonstrated on a global scale that fisheries tend to fish down the food-web as demand outweighs supply for existing fisheries (Pauly *et al.* 1998). They also discusses the dangers of a management strategy which allows for fishing down food webs, demonstrating that in some cases, in contrast to the continued increase in catch that may be expected when fishing down food webs, there may instead be abrupt phase shifts showing marked reductions or stagnation of catches. One possible explanation is that the fisheries may have induced changes in food webs through trophic cascades (Carpenter *et al.* 1985). Tracking the mean trophic level of the fishery over time may provide a useful warning indicator of potential ecosystem overfishing.

Table 25. Fisheries catch by trophic level for Lake Malawi, Fisheries Research Unit

Trophic Level	% total catch
V	3
IV	18
III	46
II	33

The mean transfer efficiencies have been calculated from trophic models applied to three contrasting African Great Lakes (Table 26). Mean transfer efficiencies between trophic levels are slightly higher in Lake Malawi than in Lake Victoria at 14.0% and 11.7%, respectively, and are significantly lower in the artificial impoundment of Lake Kariba at only 4.7%. These figures may demonstrate how energy utilisation within an ecosystem improves as the ecosystem matures and vacant niches are filled. Transfer efficiencies between trophic levels are highest between levels II and III in Lake Malawi where they reach 23%. This value far exceeds the 10% general rule for biomass transfer efficiencies between trophic levels (Slobodkin 1960) and points to highly efficient use of food resources by the primary consumers in Lake Malawi.

Table 26. Biomass transfer efficiencies for three tropical lakes, calculated from published ECOPATH models (Machena et al., 1993; Moreau et al., 1993, present model)

Trophic Level	Transfer Efficiencies (% annual basis)		
	Malawi	Victoria	Kariba
II	13.5	15.8	7.1
III	23.0	13.5	6.5
IV	8.9	7.4	2.2
V	2.9	6.1	1.9
VI	3.6	4.8	3.6
Mean efficiency of all flows	14.0	11.7	4.7
Mean efficiency of flows from primary producers	14.1	11.8	4.7
Mean efficiency of flows from detritus	13.5	10.2	4.7
Proportion of total flow from detritus	17.0	22.0	0.5

7) Assessing fishery impacts and management scenarios using ECOSIM. The parameterisation and construction of a whole-system ECOPATH model allows us to assess the impact of different fishery development scenarios and management targets and strategies on the structure and productivity of the ecosystem. Of the range of scenarios investigated in the project, we present here only a sample - the impact of doubling fishing effort, the ecological effect of aiming to maximise total yield of fish from the whole community and the yield and ecosystem effects of the on-going expansion of commercial trawl fisheries into deeper waters in southern Lake Malawi.

An initial simulation, based on maintaining 1999 levels of fishing effort for the whole lake ecosystem, was run for a 20 year period to provide the benchmark against which to evaluate simulations for alternative fishing regimes (Figure 17a). Simulations were run to predict the impact of an overall doubling of fishing yield across all gears (Figure 17b). Under current fishing pressures clariids and “Detritus and diatom Feeders” were predicted to decline and reach a stable state after about 15 years. The total catch from the combined fisheries was predicted to remain relatively constant. An overall doubling of fishing pressure (F) across all gears predicted a decline in biomass of an additional six groups, three of which - *Bagrus meridionalis*, clariids and the detritus and diatom feeding fishes - were predicted to be lost from the system.

Ecosim was next used to predict the fishing pressure increase (F) that gives the greatest total yield. A five times increase in F (assumed to occur instantaneously) was predicted to give the greatest total yield (Figure 18).

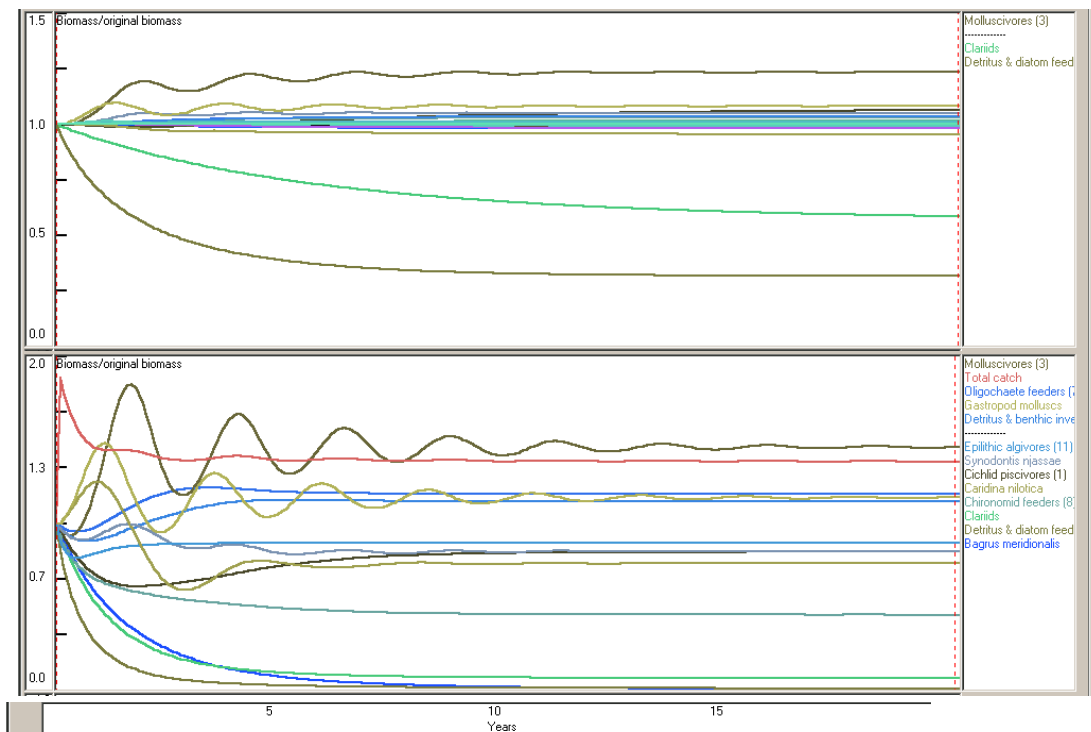


Figure 17. Predicted impact of increased fishing by all fisheries combined over a 20 year time period. Only those groups predicted to change by >10% from their baseline values are shown on the plot. (a) Baseline plot - constant fishing pressure (b) $F = 2$ for combined gears.

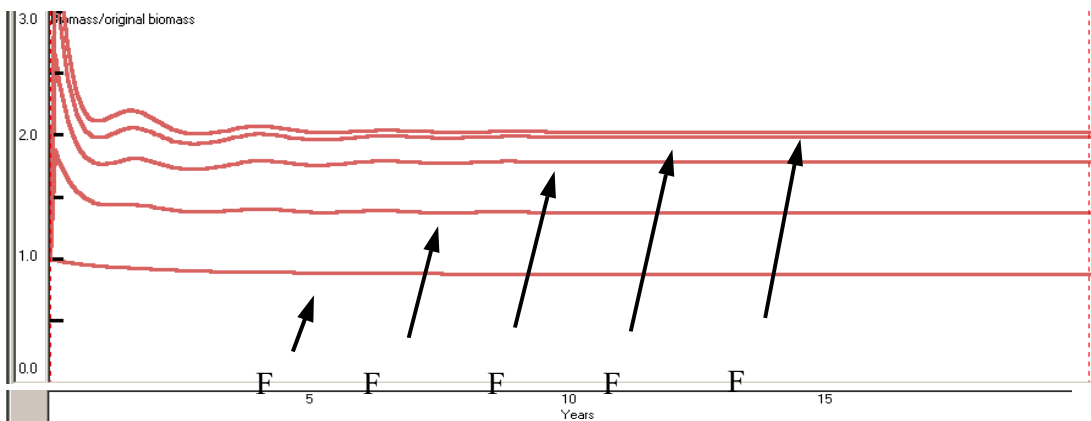


Figure 18. Whole lake model; range of F's for combined gears, where $F=1$ is current level of fishing effort, $F=2$ is double, etc.

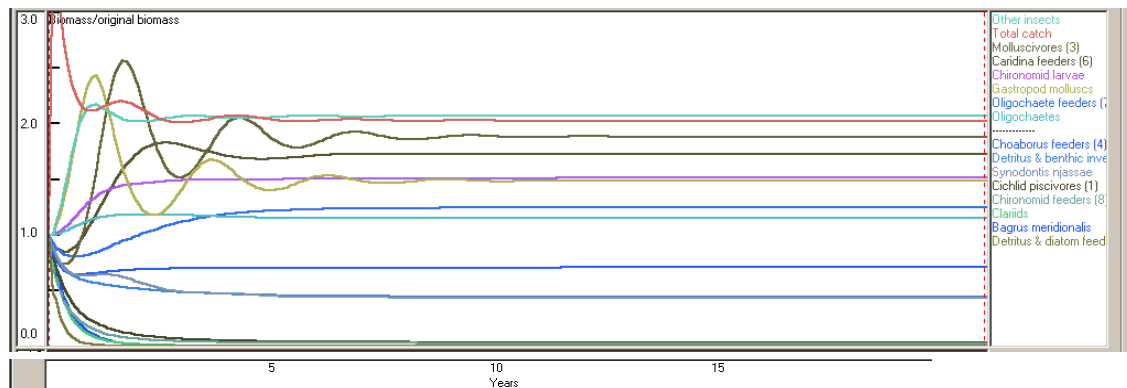


Figure 19. Whole lake model – impacts on fish trophic guilds.

The predicted impact on the fish community of a five times increase in F (Figure 19) is a simplification of the community through the loss six fish groups including *Bagrus meridionalis*, Clariids, Chironomid feeders, *Syndontis njassae*, Detritus & benthic invert feeders and *Chaoborus* feeders. This assumes that the main catch will then be dependent on Molluscivores, Caridina feeders, and Oligochaete feeders, but the change in trophic pathway implied is unlikely to occur in practice. It is more probable that the productive basis of the ecosystem would collapse before this occurs. A third example scenario simulates the impacts of further development of Malawi's commercial deep-water trawl fishery. The deep-water trawl catch was calculated to take a representative proportion of those trophic groups found at 100m and below assuming a non-selective trawl. The unexpected prediction for biomass changes following the initiation of a deep-water trawl fishery with total annual yield of $0.1 \text{ T/km}^2/\text{year}$ was an increase in biomass of *Bagrus meridionalis* (Figure 20a). This prediction was, however, reversed to a decline when the fishery total yield was raised to $0.4 \text{ T/km}^2/\text{year}$ (Figure 20b), which is slightly less than the annual yields of the existing gillnet or regular demersal trawl fisheries.

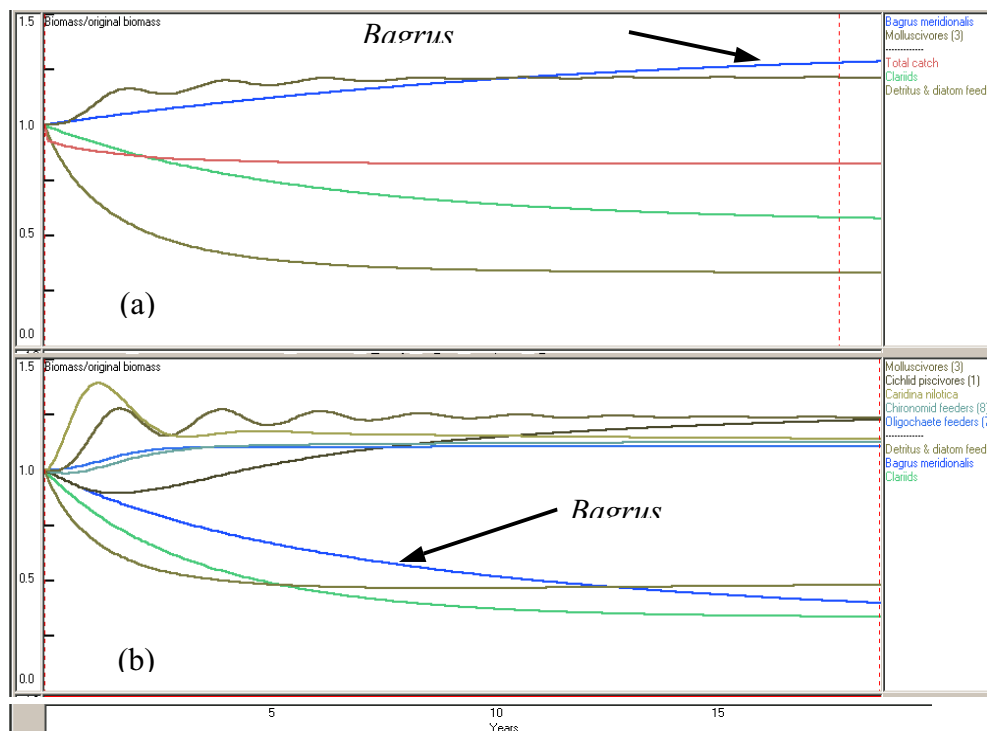


Figure 20. Predicted impact of initiating a deep-water trawl fishery of (a) $0.1 \text{ T/km}^2/\text{year}$

Although the model is useful for scenario-building, its predictions must be interpreted with caution. The model is highly sensitive to changes in prey vulnerability – a parameter that must be derived from the model or estimated from theory. Simulations with different vulnerability coefficients indicate that in most cases, the direction of predicted ecosystem change is fairly robust, but the quantitative predictions of optimal yields or fishing effort are highly sensitive to the chosen value. ECOSIM should not, therefore, be used as a tool for setting management or policy targets, but only as a means of exploring the likely ecological consequences of different policy or development options. This function needs to be combined with other tools for policy analysis (e.g. stakeholder analysis, livelihoods analysis) in management planning for the lake.

Problems encountered

1) *Stable isotope sub-contract.* The Stable Isotope sub-contract between ODG UEA and our colleagues in the School of Environmental Sciences was based on an informal trust relationship – we would be able to obtain more samples than we had budgeted for, in return for sharing the authorship of the results. Unfortunately, this informal agreement did not work in practice, and many of the samples collected remain unanalysed. As there was no formal contract between ourselves and ENV UEA regarding the minimum number of samples to be processed, we cannot legally enforce the completion of the work. Nevertheless, the work done has generated sufficient results to fulfil its original purpose as a means of validating other methods of examining trophic structure. We are seeking supplementary funding to complete analysis of the remaining samples.

2) *Parameterising ecosystem models* for one of the world's most diverse and least studied major ecosystems proved challenging, but most of the challenges were overcome. Some of the parameter values that remain a concern are those for biomass and productivity of benthic invertebrates, where the limitations of grab-sampling, and technical difficulties in developing alternative, quantitative estimation procedures make the invertebrate biomass and production part of the model rather uncertain.

Similarly, calculation of consumption biomass ratios is technically challenging. *In situ* calculations have to contend with the fact that a portion of fish stomach contents are likely to be lost due to the pressure change on being brought to the surface from depth. This pressure effect will be considerable for both trawling depths employed in this study. Attempts to select individuals that had retained their stomach contents may not have been wholly successful with partial evacuation being a possibility. This could explain the low Q/B values relative to those obtained by the empirical method. A second potential problem with this technique applies to those species, such as piscivores, which rely on the occasional consumption of a few large prey items.

3) *The estimates of demersal species composition* would have been more precise if we had been able to carry out a larger number of lake-wide research cruises. Hire of the RV Usipa proved to be more expensive than we had anticipated, and we were only able to carry out 3 cruises, rather than the four planned. Furthermore, one of these cruises had to be abandoned because the trawl net was damaged on a sunken tree while fishing the uncharted waters off Mozambique. However, access to data

collected by the FRU and SADC/GEF projects largely compensated for these problems. We did not collect data on seasonal changes in fish communities, fish diets, reproduction and growth because we were aware that this was concurrently being carried out by the SADC/GEF project (Duponchelle & Ribbink 2000).

4) Completion of the project proved problematic, as while waiting for data for parameterisation of models, UEA ODG staff had to become involved with other programmes, which imposed their own deadlines. This partly explains the delay in overall reporting, and we are aware that these commitments have in turn led to delay that has contributed to the lateness of the final reporting process.

These technical and administrative problems were by far outweighed by the success of the project in generating one of the more comprehensive ecological datasets on the world's great lakes.

Publications and papers

- Allison, E.H. (2002). Sustainable management in the African Great Lakes: Science for development? *Aquatic Ecosystem Health & Management* 5(3): 313-325. ISSN 1463-4988
- Allison, E.H., P. M. Mvula and F. Ellis (2002). Competing agendas in the development and management of fisheries in Lake Malawi. In K. Geheb & M-T. Sarch (Eds). *Africa's Inland Fisheries: The Management Challenge*. Kampala, Uganda: Fountain Books, pp 49-88. ISBN: 9970 02 293 8.
- Darwall, W. & E.H. Allison (2002). Monitoring, assessing and managing fish stocks in Lake Malawi: Current approaches and future possibilities. *Aquatic Ecosystem Health & Management* 5(3): 293-305. ISSN 1463-4988
- Darwall, W.R.T., (in prep). Spatial structure and trophic ecology of the Lake Malawi Demersal Fish Community". PhD thesis, University of Hull, U.K.

Conclusions

Trophic and modelling studies have led to a number of important insights that will help to guide future management of Lake Malawi fisheries and biodiversity.

1. The high proportion of trophically equivalent taxa within the Lake Malawi demersal fish community could be important for maintenance of ecosystem function through provision of a buffer against environmental change. The level of resilience provided by the buffering effect will depend upon the width of environmental tolerance stored within the genetic composition of these taxa. It would therefore be both risky and foolish to allow these taxa to be lost. The fisheries manager who is prepared to fish in a way that allows the elimination of all "redundant" buffering species is equivalent to the investment managers who put all his faith in a single stock. Should conditions change, all investment in a single stock may be lost. Similarly, should environmental conditions change, without the buffering effect of "redundant species" the fishery may fail to adapt and collapse.

2. The proposed role of lakeflies (*C. edulis*) larvae in the ecosystem has been somewhat clarified. Allison *et al.* (1995) showed that *C. edulis* was a more important food source to the pelagic fish community than originally suggested by Degnbol (1993), and went on to propose that demersal fish might also rely on consumption of *C. edulis* larvae. The integration of the demersal and pelagic systems within the current model shows that approximately 50% of *C. edulis* production is directly consumed by pelagic fish and a further 4% by demersal fish. The remaining 46% of

production either flows to detritus, where a certain proportion will be recycled through detritivores, or leaves the system through dispersal as flying adults (some of which return to the lake and are consumed by surface-feeding catfish). The actual proportion of production lost by adult dispersal still needs to be determined but is significantly lower than Degnbol's original estimate of more than 60% of total production (Degnbol 1993).

3. Although the model shows that *C. edulis* does indeed provide a direct link between the demersal fish community and pelagic productivity it is now clear that the main pathway for energy flow is through the consumption of copepods by demersal fish apparently migrating into the pelagic for feeding.

4. By integrating the demersal and pelagic components of the Lake Malawi ecosystem into a single model, it has been shown that the lake is much more efficient than previously supposed (e.g. Hecky, 1984) as the demersal fish community is able to directly utilise much of the pelagic production previously thought to be exported to detritus.

5. Scenario modelling shows that current fishing levels will lead to trophic change, as well as species change. Increasing those levels of fishing (as is likely under the current pressure on stocks and the lack of enforcement capacity) will cause further change in both species composition and trophic structure, although total fish yields may continue to increase, particularly if fishing is expanded into areas where there is currently a low level of fishing effort (the deep water demersal and offshore pelagic zones).

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Partner 6: University of Southampton, School of Biological Sciences (USOU.DBE)

Reporting Scientists: George Turner; William Darwall.

Objectives

Frame survey of fishery gears and catch; collation of existing fishery statistics, close links with partners UEANG.ODG and TANZ.FRI in fishery assessment and with partners UHULL.DBS.FG and UMW.DB for taxonomy. Recent connections with fishery dept. Mozambique will facilitate collection of data along the Mozambique shoreline. The involvement of USOU.DBE was towards the attainment of Task 5.

Scientific Activity Report

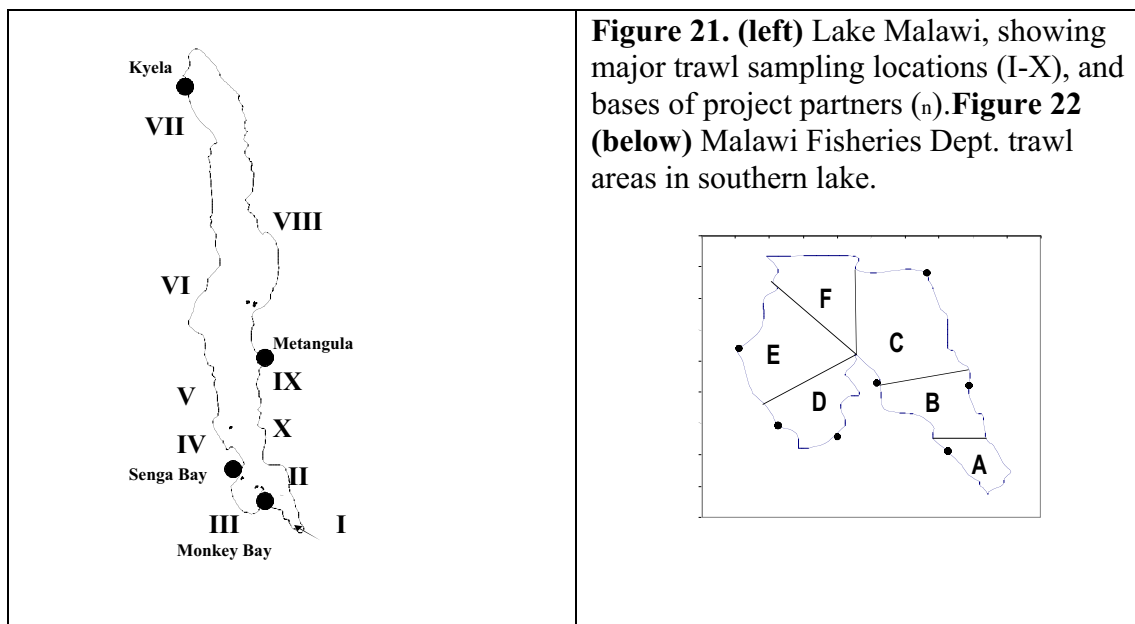
The input by USOU.DBE to Task 5 of the project included 18 months full-time employment by one research associate (Mr W. Darwall) and provision of advice in the design of frame surveys and surveys of artisanal and commercial fisheries and fish stocks implemented by the FRU and NARMAP, by the Tanzanian Fisheries Research Institute (TANZ.FRI) and by two MSc candidates seconded from the Mozambican fisheries department (associated scientific partner) to the SADC/GEF Biodiversity project. This involved visits by Mr Darwall to Tanzania and Mozambique to participate in the establishment of artisanal fisheries surveys and in staff training programmes. To assess the species composition of the demersal fish communities, we implemented three lake-wide research trawl cruises (major sampling sites shown on Fig. 21) and participated more local surveys carried out by the GEF project and the Malawi fisheries dept. These surveys also provided data on fish diets (report by partner UEANG.ODG) and invertebrates (partners UDTC.DZ & IRSNB.FBL), and samples for fish genetic and taxonomic studies (partners IRSNB.FBL, MRAC.LI, UHULL.DBS.FG and UMW.DB). In addition, we reanalysed data sets previously collected by the Malawian Fisheries Dept (MNRMW.FD.FRL) and collaborating projects to assess temporal changes in fish community structure and species composition in relation to fishing practices.

Results Achieved

Frame Surveys

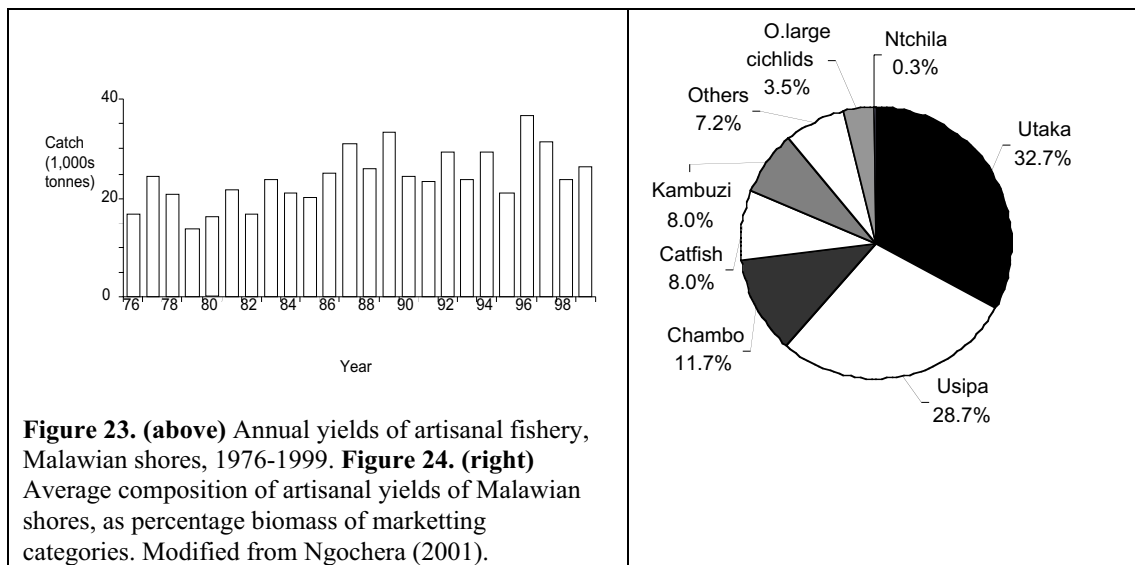
A frame survey is performed to estimate the fleet size and composition of an artisanal fishery. Additional data recorded can include gear dimensions and socioeconomic data. As well as providing important indicators of the health of the fishery in its own right, frame surveys are essential to provide raising factors to estimate fishery effort, when combined with catch per unit effort (CPUE) data. The Malawian sector of the lake was found to have been well covered by the existing frame surveys which have been run since 1976. However, economic contingencies had led to the suspension of the survey for several years. Fortunately, we able to provide partial funding to assist in resumption of the survey. In Tanzania fisheries statistics had hitherto been collected by the Fisheries Department and not the Tanzanian Fisheries Research Institute (TAFIRI). As far as could be determined, no frame survey had ever been

carried out on the Tanzanian sector of the lake, which in itself suggests that previous catch returns from the Tanzanian part of the lake may be unreliable. After extensive discussions between Mr Darwall and staff from TAFIRI, a frame survey was designed and carried out on the Tanzanian shores. The report on this survey is provided by TANZ.FRI. In Mozambique at the time of initiation of the project, there was no governmental fisheries infrastructure on the Mozambican side of the lake, and very little fishing activity. The situation was only marginally improved by the time of cessation of our fieldwork in 2000. However, we did manage to advise on the conduct of a full frame survey of the Mozambican shore carried out under the GEF project in 2000 by Mr Jorge Mafuca (ecology student on the Lake Malawi GEF Project). The results of this survey have been deposited at the GEF project base in Senga Bay Malawi. Survey sites are shown in Figures 21 and 22.



Artisanal Fishery Catch Sampling

Considerable progress was made in synthesising artisanal fish catch sampling data from Malawi. Artisanal fishery yields were found have been approximately stable for the last 15 years (Fig. 23). Lake-wide, the Malawian artisanal fishery continues to be largely dependent on small low-value zooplankton-feeding cichlids (Utaka) and cyprinids (Usipa). Yields of the higher value catfish and tilapias (Chambo) have declined, and now comprise less than 20% of the total catch. The river spawning cyprinids (ntchila etc) are presently of very low importance probably as a result of high targetted fishing effort, but also disturbance of the river catchments by agriculture. In collaboration with FRU, Malawi and the GTZ-funded NARMAP programme, the project developed a catch-sampling programme that recorded catches to species level, thereby enabling the breakdown of national statistics collected by aggregate marketing categories (Fig. 24) into their likely biological species composition. These were then be re-aggregated for the modelling studies, according to the functional groups identified through analysis of trophic guilds (see report by UEANG.ODG) and other assembly rules drawn from community ecological studies.



Fisheries catch-effort and species-composition data were also obtained from a one-year sampling programmes in Metangula, Mozambique and along the Tanzanian coast. These fisheries were largely dependent on mid-water feeding species, such as the small cyprinid *Engraulicypris sardella*, zooplankton-feeding inshore cichlids (*Copadichromis spp.*) and the pelagic cichlids (*Rhamphochromis* and *Diplotaxodon*). River-spawning species, especially cyprinids, were more important than on the more densely populated Malawian coasts, probably owing to lower fishing effort and lesser disturbance of the Mozambican and Tanzanian river catchments. Demersal species were far less important than in the southern Malawian shelf areas.

Appraisal of artisanal fisheries stock assessment methods

The ultimate objective of most fishery management is to obtain the maximum yield (economic or biomass) of fish that can be sustained over time. It is now recognised that in most of the world's managed fisheries this has not been achieved. In less developed countries, particular problems arise when the management approaches recommended are too 'data hungry' and consequently expensive to implement (Mahon, 1997). The adoption of inappropriate monitoring strategies, such as advocated in many of the most widely available manuals on fishery management, can lead to a serious imbalance in the use of limited funds such that mountains of data are collected but no funds are left to analyse them and, most significantly, act on the advice generated. The fisheries of Lake Malawi, although important (est. 35-40 000 t annual yield), have to be managed on a limited economic base. We examined the current management of fisheries in Malawi's waters (where the only reasonable data time-series exists) and discuss ways of obtaining a better match between the available human and economic resources and the management strategy adopted.

The fishery in Malawi is largely of a small-scale non-mechanised nature with a mechanised trawl fishery operating in the southern part of the lake. The fishery mainly employs paddle-powered dugout canoes, fishing gill and seine nets, handlines and longlines, and basket and fence traps. Recent records estimate the total yield from the small-scale fishery to have fluctuated around 30,000 tons over the last ten years. The total catch of trawl and ringnet fisheries has been around 4-5 000 tons per annum.

Some of the key fish stocks are declining, fish community compositions are changing and fishing effort is rising rapidly. This situation, combined with the time lag in data analysis and the lack of enforcement, leaves the fisheries in a highly vulnerable state. An effective assessment and management strategy is needed urgently.

In 1976, on the advice of FAO, the Department of Fisheries opted for a 'Stock Assessment Driven' (SAD) approach to fisheries management (Mahon, 1997) and a long-term programme of routine catch monitoring was initiated. The monitoring of the trawl fisheries relies on the fisheries operators submitting, to the Department of Fisheries, catch and effort records on a monthly basis. The submission of these records is a condition of the granting of the license to fish. The small-scale fisheries are monitored through the combination of a boat-based 'Catch Assessment System' (CAS) developed by Bazigos (1974) and introduced in 1976, and a gear-based system - the 'Malawi Traditional Fisheries' system (MTF) introduced to the Mangochi District in 1990 by FAO (1992). Total fishing effort is assessed through annual Frame surveys at all landing sites throughout the Malawi sector of the lake. The CAS requires monthly surveys of fish catches and fishing effort at four randomly selected landing sites within each of 33 minor strata distributed along the full length of the Malawi shoreline. Beach recorders spend four days a month at each landing site such that 16 days in each month are spent in catch recording. On the first day at each site the recorder carries out a census of the numbers and types of craft and fishing gears present. For the next three days, catch and effort data are collected from selected fishing boats. Boats are selected, using random numbers, on the basis of their order of arrival at the landing beach. Catch is assessed by weight for a total of 13 different 'species groups'. Fishing effort relating to each catch is recorded as the number of fishermen and the number of hauls (seine nets), length of headline (gillnets), or number of hooks (longlines and handlines). The data recorded are then sent to the District Fisheries Office for manual processing and summarising before being sent on to the Fisheries Research Unit for estimation of total catches and fishing effort. The CAS has no protocol for ensuring that the full range of gear types is surveyed equally. The basic data collection procedures of the MTF are similar to those of the CAS but the system is 'gear-based' such that total yields are obtained through multiplication by the number of active gears rather than the number of boats. This provides an improved yield estimates. The MTF system allows for direct input to computer of raw data for statistical analysis, and catch yields are calculated using raising factors that account for any bias associated with catches from small beaches. The annual Frame survey of fishing gears and fishing effort is normally carried out during the months of August or September in the dry season when most landing beaches are accessible. The survey involves visits to all landing sites along the shore to count fishermen, their gears and fishing craft. The results of the survey are used in conjunction with the data from the CAS or MTF to estimate total monthly landings and fishing effort for all traditional fisheries along the lake.

Stock management advice has, until recently, been based upon an analysis of time series of CPUE data to determine maximum sustainable yields through use of surplus production models. Subsequent management recommendations have been largely based on technical restrictions on fishing gears and restrictions on fishing areas or times, and minimum size of first capture. In recognition of the shortcomings of surplus production models the Department of Fisheries has recently recommended adopting a 'precautionary approach' where a level of CPUE is selected below which

catch rates should not be allowed to drop (Bulirani *et al.*, 1999). The threshold level of CPUE has been called $CPUE_{pa}$, calculated as 45% of $CPUE_{max}$ which, in the absence of stock estimates for virgin biomass, is the mean CPUE over a period of five to ten years of relatively high CPUE. Effective management of the fisheries has, however, been extremely limited owing to a lack of finance and manpower for the enforcement of these policies. The same lack of manpower and finance has also left much of the catch and effort data unprocessed. The backlog in data analysis has limited the reporting of outputs from Frame surveys to once every 4-5 years and by 1999 the analysis of time series for CPUE was three years in arrears. In consequence, any decline in catch rates would be unlikely to be detected in time for management action.

In summary, the failures of current management appear to have arisen partly through an imbalance in the allocation of resources to data collection and to data analysis and enforcement. A more structured approach is needed to refine the existing stock-assessment based management system.

The combined Lake Malawi fisheries exploit in excess of 300 species of fish which exhibit a broad range of life history traits that may respond in significantly different ways to fishing pressure. A single species management approach would therefore be inappropriate and many of the multi-species, multi-gear and ecosystem approaches are likely to prove too costly. The choice of management strategy is therefore not obvious. We suggest that several fundamental issues need to be clarified. 1. Management objectives must be clarified – is the fishery to be managed principally for maximum economic yield, for maximum biomass yield, for sustaining livelihoods for as many fisherfolk as possible, for conservation of diversity, or for a combination of these? 2. The level of available management resources (human and economic) must be determined. 3. Potential options for management strategies and their data requirements and costs should be determined. 4. A management strategy should be chosen which can meet the management objectives while remaining within the limits of the economic and human resources available for its implementation.

In addressing the question of management priorities, the frequency of quoted statements such as ‘the lake fisheries provide up to 70% of the country’s dietary animal protein’ would suggest that the priority is to maximise protein production or fish biomass yield rather than economic yield. There has, however, been criticism that Malawi Fisheries Department and donor support have favoured the industrial, more profit oriented, sector over the small-scale or traditional sector. According to Bland and Donda (1994) fishery sector policy objectives are to maximise the sustainable yield from fish stocks, improve efficiency of exploitation, processing and marketing and exploit all opportunities to expand existing, and develop new aquatic resources, while taking care to protect species biological diversity. There has been much less explicit consideration of fisheries policy with respect to issues of employment, equity and resource allocation within the catching sector. It therefore remains unclear whether the Department of Fisheries management policy favours a drive towards economic gains or high protein yields. Although biological diversity within the lake is highly valued internationally and fisheries sector policy does state the intention to conserve biodiversity, the higher priority of the country will be to feed its people and generate income from natural resource exploitation. Biodiversity is therefore only

likely to be preserved, (unless additional external funding is provided) if it can be linked to the maintenance of productivity of the fisheries.

The revised Malawi Fisheries Act (1997) sets out legal provision for 'community-based management'. The design of appropriate management institutions is hindered by the difficulties in designing village-based fishing territories for fisheries that include migratory fish stocks, traditionally exploited opportunistically by migrant fisherfolk. There are also difficulties regarding representation of fishing and other interests on the new management institutions – the beach village committees. Although a promising development, it would seem premature to abandon the existing state-based management system at this stage, or even cease to consider improvements to it. A continuation of the current approach, based on the combined use of CPUE_{pa} and surplus production models provides the most appropriate option but we suggest a number of significant modifications.

The current stock assessment based management approach could be significantly improved through a major cut back in the scale of data collection and a lakewide switch to the use of the MTF system (where data are entered directly onto computers, rather than requiring a great deal of transcription and manual calculation), possibly incorporating the database under development by NARMAP. Attention needs to be directed towards an appraisal of the precision of fleet size estimates derived from the frame surveys, possibly through repeated re-sampling on a small area. These actions should help to reduce errors in data collection and free up personnel and financial resources to ensure timely analysis of the data and the implementation and enforcement of management recommendations. Consideration should be given to the inclusion of locally based fisherfolk in the catch monitoring program (which we have piloted in Tanzania and Mozambique). Such a move would provide benefits in the form of improved use of local knowledge and reduced running costs such as associated with transport and lodgings for beach recorders. These actions should assist in meeting the broader target of sustainable management of fisheries.

Research trawling: Research trawling to assess biomass and species composition of demersal fish was completed in January 2000. Three lake-wide trawl surveys and three more localised surveys were conducted using the RV Usipa. This data was supplemented by analysis of trawl data held at the Monkey Bay Fisheries Research Unit. Analysis of mean catch rates for all sites (Fig. 25) indicates that although high catches were made in individual tows in the central and northern lake, catches in the heavily exploited southern part of the Lake (Areas I-III) were not significantly lower. This may be due to the higher natural productivity of these areas. There was no consistent trend with bottom depth. The results for Areas VII-X have high variability as they are based on small sample sizes.

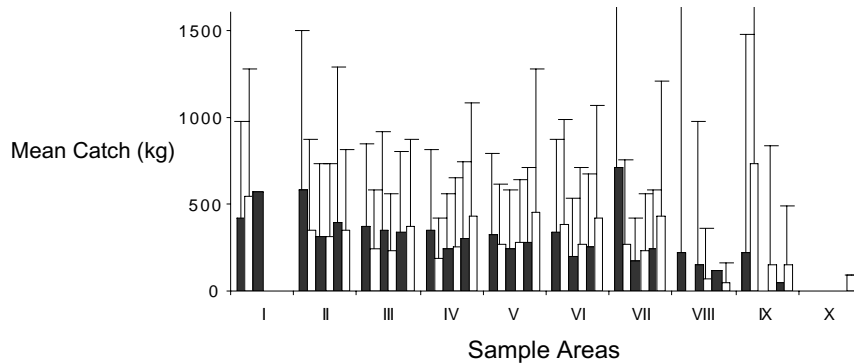
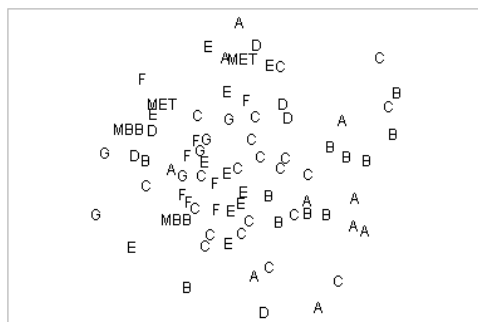


Figure 25. Mean biomass (kg) and 95% confidence limits of trawl catches by depth bands, based on 406 trawl hauls, mean/std = 8.12 ± 4.63 per category represented. For each sample area, depth ranges are presented separately (from left to right): 0-20m, 21-40m, 41-60m, 61-80m, 81-100m and >100m.

Preliminary analysis using four common diversity indices (of which the Simpson-Yule was most sensitive and Shannon-Weiner diversity index least sensitive) consistently found the highest fish community diversity at the shallowest and deepest areas of the heavily fished South-East arm of the lake, and along the relatively unfished Mozambique coast. No clear patterns are evident on the basis of geographic location or water depth.

Location Effects 98-99 data 0-20m: untransformed data



Location Effects 98-99 data 0-20m: 4th root transformed data

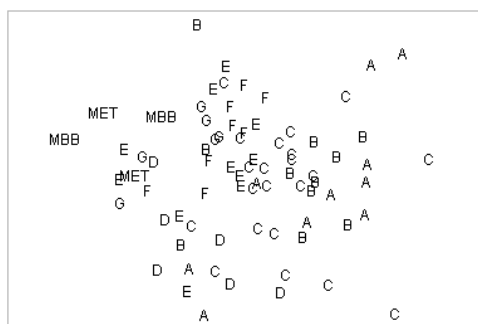


Figure 26. Multidimensional scaling plot of species compositions for all experimental demersal trawl catches, using untransformed (left) and 4th-root transformed (right) % biomass data. Letters A-G refer to trawling areas I-VII, MMB to VIII, MET to IX.

A clear gradation in community structure with sample area became more pronounced with the increasing severity of the data transformation from "no transformation" to the most extreme transformation to "presence absence" data (Fig 26). As the effect of the transformations used is to increasingly reduce the influence of abundance or dominance effects until only species presence or absence is recorded it is clear that the main effect must be due to species replacements rather than changes in the relative abundance of species between areas. The significance of similarities between areas was evaluated using ANOSIM (analysis of similarities) which computed global R statistics for analysis of the untransformed, $\sqrt{}$, $\sqrt{\sqrt{}}$, and presence / absence transformed data for the 0-20m depth band of 0.216, 0.278, 0.287, and 0.26, respectively, all of which were significant at the level of $P < 0.001$. The 21-40m depth band gave R statistics of 0.491, 0.602, 0.63 and 0.618. The $\sqrt{\sqrt{}}$ transformation provided the highest R statistic for area differences for both the 0-20m and 21-40m depth bands. The $\sqrt{\sqrt{}}$ transformation, which significantly reduces the influence of dominant species, was therefore chosen for the analysis of all other depth bands.

The effect of removing the less abundant species from the analysis was investigated, because it was thought possible that the "hit-and-miss" effect of sampling rare species may confuse the MDS picture distinguishing the main groupings. However, the best resolution of groupings was obtained when all species are included, suggesting that the less common species contribute significantly to differences between sampling areas. Complete data sets were therefore used in the analysis of all depth bands.

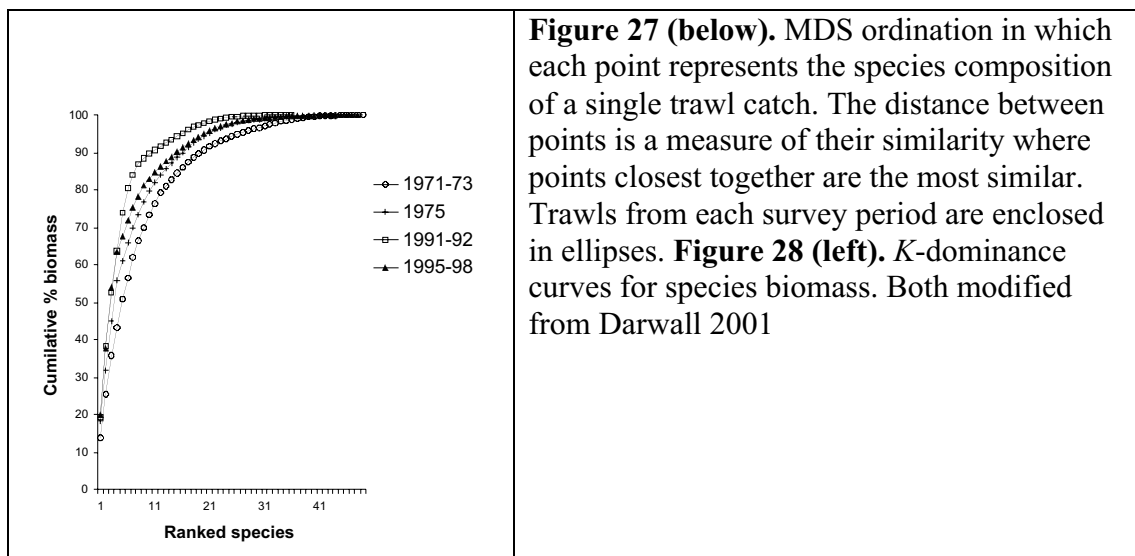
The significance of the R values was calculated using a "permutation test". Sample areas were found to have significantly different communities at all depths. As the MDS plots indicate, community compositions appear to become more divergent with increased distance apart such that the community composition in Area I is very different to that in Area VII at the opposite end of the lake. One would expect community divergence to be greatest in the shallower depth bands where effects such as habitat heterogeneity and human impacts such as from fishing would be greatest. However, the Global R values for each depth band do not decrease with depth although the 21-40m depth band shows the greatest difference of all depths. In most cases communities in adjacent areas were not significantly different. Communities at Mbamba Bay (area VIII) and Metangula (IX) were notably different from each other and all other areas although, in most cases, the small sample sizes for these areas probably precluded these differences from being statistically significant. However, the largest samples for these two areas, obtained in the 100+m depth band, were found to be significantly different from most other areas at the 1% level although the two areas themselves were still not significantly different despite their relatively high R value (0.481).

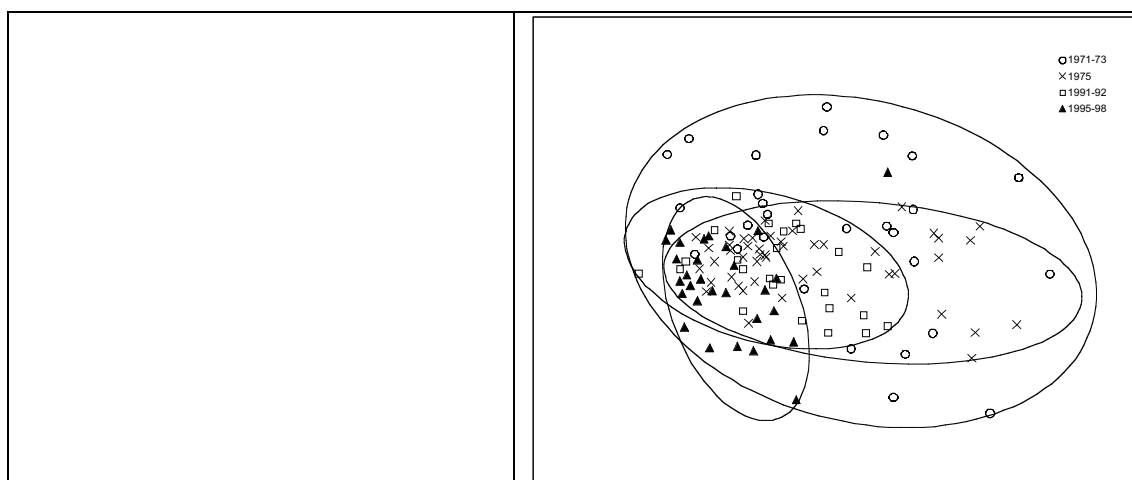
While the limitations of the sample size pose certain problems for the analysis of ecological community structure and measures of biodiversity, they are less problematic for studies of gross community structure, as required for analysis of trophic structure, and for fisheries assessment. This is because the common species are well represented, and 'missing' species that could be present in larger samples are invariably rare species that contribute little to fisheries catches or overall biomass and energy flows in the benthic ecosystem.

Temporal Changes in Demersal Fish Communities

Previous studies (FAO 1976; Turner *et al.* 1995) have reported significant changes in the demersal fish community following the initiation of industrial trawling in 1968, particularly in the heavily exploited Area A (Fig. 21). We investigated community level responses in the demersal fish fauna of Area A throughout the thirty year period of benthic trawling. Species compositions were obtained from experimental trawl surveys conducted by the Malawi Fisheries Research Unit (FRU) since 1970. Inconsistencies in taxonomic identifications and catch sampling methodologies combined with the replacement of the research vessel Ethelwyn Trewavas with the RV Ndunduma in 1993/4 necessitated extensive standardisation of data. In recognition of the differences in catch compositions from the two vessels all shoaling 'off-bottom' species (*Copadichromis*, *Diplotaxodon* and *Rhamphochromis* spp.) which would be caught preferentially by the Ndunduma were excluded from the analyses, as were the larger, faster swimming species (the 'large fish' portion of the catch). As all species compositions are presented as percentages of total biomass, standardisation of trawling times and swept areas was not required. Dominance curves, diversity indices, and Multi-Dimensional Scaling (MDS) ordination techniques were used in the analyses of temporal changes in community composition. MDS ordinations were based on Bray-Curtis Similarity matrices of 4th root transformed percentage biomass for each species. The sample unit was taken as an individual trawl catch.

MDS ordination demonstrated a clear temporal reduction in diversity between catches (Fig. 27). Within a survey, trawl catches are becoming more similar (mean similarity 38.89 in 1973 and 54.28 in 1998 - Bray-Curtis similarity index). K-dominance curves show that the community has become dominated (in terms of biomass) by fewer species in recent years (Fig. 28). There was no significant reduction in species richness over time, at the restricted taxonomic level used in the analyses. The trend for increasing dominance was reversed during the last survey period (1995-98). This apparent reversal towards the original state of evenness may indicate a degree of community resilience to fishing.





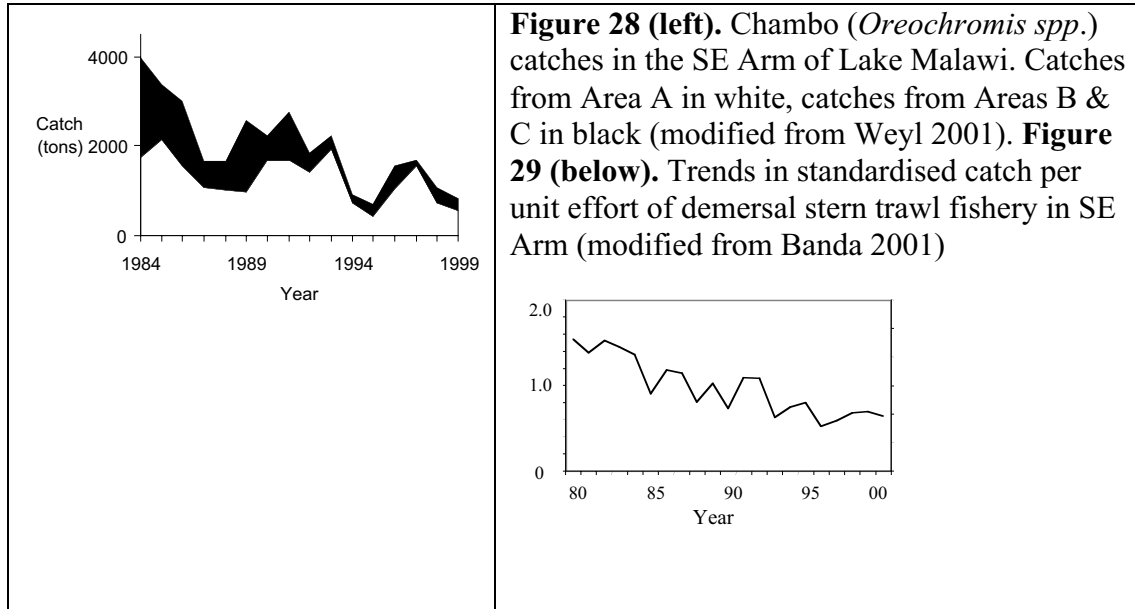
However, detailed analysis of the species composition indicated that populations of several 'key indicator' species had not only failed to recover since the early 1990s, but in some cases there was evidence of further declines (Tables 27 & 28). Of the four most severely affected species, three (*Lethrinops mylodon*, *L. macracanthus* and *L. microdon*) were recorded from experimental trawls to the north of the southern arms. This indicates that data recorders are still able to identify these species. Furthermore, these species appear to be persisting in areas where trawling is presently light or absent, and to have disappeared from heavily trawled areas. This makes it highly probable that expansion of trawling in the northern areas of Lake Malawi will lead to the extermination of these species. The decline of these large haplochromine species is mirrored by the decline in catches of the large *Oreochromis spp* (Chambo) despite increases in fishing effort (Fig. 29). *Oreochromis spp.*, *Lethrinops microdon* and *L. stridei* all feed mainly on sedimented diatoms. The fishery is now becoming more dependent on small invertebrate feeders rather than larger algal feeders, and so seems to be a rare example of fishing up, rather than down the food web. It is possible that the decline of these species may be an indirect effect of trawling, resulting from churning of bottom sediments. Trends in the demersal trawl fishery are not encouraging (Fig. 29). It is also possible that the decline in *Oreochromis* may be due to artisanal fishing on the juveniles which are found in shallow areas vulnerable to seining. This is believed to have caused the decline of *Oreochromis* in the neighbouring Lake Malombe (FAO 1992).

Table 24. Population changes (as % biomass from experimental trawls) in key indicator species Area A

Species	Characteristics	71-2	75	91-2	98-9
<i>Lethrinops mylodon</i>	25cm TL molluscivore	0.3	0.01	0	0
<i>Lethrinops stridei</i>	16cm TL diatom feeder	8.1	2.9	3.9	0
<i>Lethrinops macracanthus</i>	25cm TL chironomid eater	3.1	0.1	0	0

Table 25. Population changes in key indicator species Areas B & C

Species	Characteristics	71-2	73-5	91-2	98-9
<i>Lethrinops macracanthus</i>	25cm TL chironomid eater	2.6	1.3	0	0
<i>Lethrinops microdon</i>	20cm TL diatom feeder	16.2	13.3	1.9	0



Publications and papers

Outputs from W. Darwall reported by partner 5.

Conclusions

Tanzania and Mozambique now have the trained personnel to successfully implement catch assessment and frame surveys of their artisanal fisheries, provided funding is made available. Although no time series are available, it seems the fisheries are lightly exploited and expanding.

Fishery yields in Malawi are not expanding, and several key stocks are in decline. We suggest that a streamlining of the catch assessment survey can lead to diversion of resources towards more accurate and timely data analysis and to implementation of management strategies.

Demersal fish communities are not more diverse and biomasses are not higher in the lightly fished areas. This is probably because the heavily fished areas are naturally more productive and had more diverse communities. In heavily trawled areas, community compositions have exhibited marked changes with time, and although community-level parameters indicate resilience, populations of vulnerable species continue to decline. Expansion of trawling is likely to lead to lake-wide collapse of the populations of such species.

Problems encountered

The estimates of demersal species composition would have been more precise if we had been able to carry out a larger number of lake-wide research cruises. Hire of the RV Usipa proved to be more expensive than we had anticipated, and we were only able to carry out 3 cruises, rather than the four planned. Furthermore, one of these cruises had to be abandoned because the trawl net was damaged on a sunken tree

while fishing the uncharted waters off Mozambique. However, access to data collected by the FRU and SADC/GEF projects largely compensated for these problems. We did not collect data on seasonal changes in fish communities, fish diets, reproduction and growth because we were aware that this was concurrently being carried out by the SADC/GEF project (Duponchelle & Ribbink 2000).

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Partner 7: University of Malawi, Chancellor College, Department of Biology (UMW.DB)

Reporting scientist: Aggrey Ambali

Other contributors: Wisdom Changadeya

Objectives

The Biology Department at Chancellor College was one of the partners on task 4, fish taxonomy. Its primary contribution was to map the genetic distribution of commercially exploited cichlids. This information would complement the species identification using morphometrics, which was carried out by other partners on the task 4. The work at Chancellor College was based mainly on microsatellite DNA analysis using an ABI Prism 310 Genetic Analyser. To accomplish this, work was done under a title, Zoogeographical Distribution and Population Structure of *Taeniolethrinops praeorbitalis* exploited by Artisanal Fishermen in the Inshores of Lake Malawi. This study was necessary because it was not known, until this study, as to how much genetic diversity existed in the species in various parts of the lake and the degree of population structuring that had taken place over the years. This information is useful for making management decisions for sustainable utilization and conservation of the species.

The main objective of this study was to develop predictive genetic conservation and management procedures for sustainable utilization and conservation of commercially important cichlids in Lake Malawi.

Specific objectives of the study were:

1. To determine the distribution of *T. praeorbitalis* in central and southern Lake Malawi based on artisanal fishermen catches.
2. To determine the genetic diversity of *T. praeorbitalis* in various sites of the lake.
3. To determine the population structure of *T. praeorbitalis*.

Scientific Activities

An annual landing of about 33,000 tonnes of fish is realized from inshore shallow areas of Lake Malawi, thus making traditional fisheries generally important along the coast of the lake. *T. praeorbitalis* is distributed over open sand in shallow water to a depth of not more than 50 metres. Different depth distribution ranges have been reported within and slightly above 50 meters. This study was carried out at the Molecular Biology and Ecology Research Unit (MBERU), AMBAKA Building at Chancellor College. Some studies of fish genetics of Lake Malawi stocks have been done in the past but the specimen were analysed in foreign DNA laboratories due to lack of DNA laboratory and expertise in the country. Under this study, a Malawian graduate student (Wisdom Changadeya) was recruited in July 1998 and attended course work. In 1999 the student was sent to Japan for 2_ months to be trained in fish phylogeny and DNA analysis. This training was done in DNA laboratories at Fukui Prefecture University and Tokyo Institute of Technology. When he returned, he

carried out laboratory work and generated data for his master thesis. He graduated in November 2001 with a Masters of Science in Biology from the University of Malawi.

Methodology

Literature review was done in the Chancellor College Library, Domasi Aquaculture Centre Library, Salima SADF/GEF Library and MBERU Resource Centre. The information obtained was on *Lethrinops* spp. catches, importance of artisanal fisheries, biology and distribution of *T. praeorbitalis* and other relevant information.

In 1998, the MBERU team conducted surveys to characterize the sampling sites of *T. praeorbitalis*. During these surveys, we identified fish landing docks where this species was readily found in Nkhota-kota, Salima and Mangochi districts. Pictures of the species was also taken using digital camera to facilitate identification during sampling. Gillnets and seine nets were identified as the main fishing gear that the artisanal fishermen used to catch the species.

In 1999 *T. praeorbitalis* specimen were collected from fish landing docks in Nkhota-kota District, in the central region, and Mangochi district, in the southern region. Tissues of about 5-10 mm² were extracted using scalpels from each fish and preserved in 95% ethanol in vials, which were properly labeled. Later the specimen were stored under 4 °C. Figure 29 shows sampling sites.

DNA was extracted from fish muscle tissues of 3mm² using standard DNA extraction procedures. The extracted DNA was quantified using UV-1601 UV-Visible Spectrometer and diluted to 25ng/μl, which was the desired DNA concentration for pcr. Six microsatellite loci ((UNH 130, UNH132, UNH154, UNH 146, UNH201 and OS64) were employed for amplification of DNA during Polymerase Chain Reaction (PCR). Amplified PCR products were analysed on a capillary-based ABI 310 Prism Genetic Analyzer following a protocol outlined by the manufacturer.

Allele size data obtained from the genetic analyzer were analysed using Genepop Version 3.3 software. The following analyses were conducted: test for conformity to Hardy-Weinberg Equilibrium, Test for genotypic linkage disequilibrium, test for genic differentiation and estimation of effective number of migrants. Poptools Version 1.31 software was use to compute a number of measures of genetic variation within and between sample populations, the variables being; observed and effective number of alleles, observed and expected heterozygosity, Shannon Information Index and Wrights statistics. Mantel's test was carried out determine the correlation between geographical distance and Rho-ST values between populations and the MXCOMP program of NTSYS was used to compute a product-moment correlation coefficient for two distance matrices. Genetic relationship among the populations was analysed by a multidimensional scaling (MDS) of the Nei's (1978) Unbiased Genetic Distances.

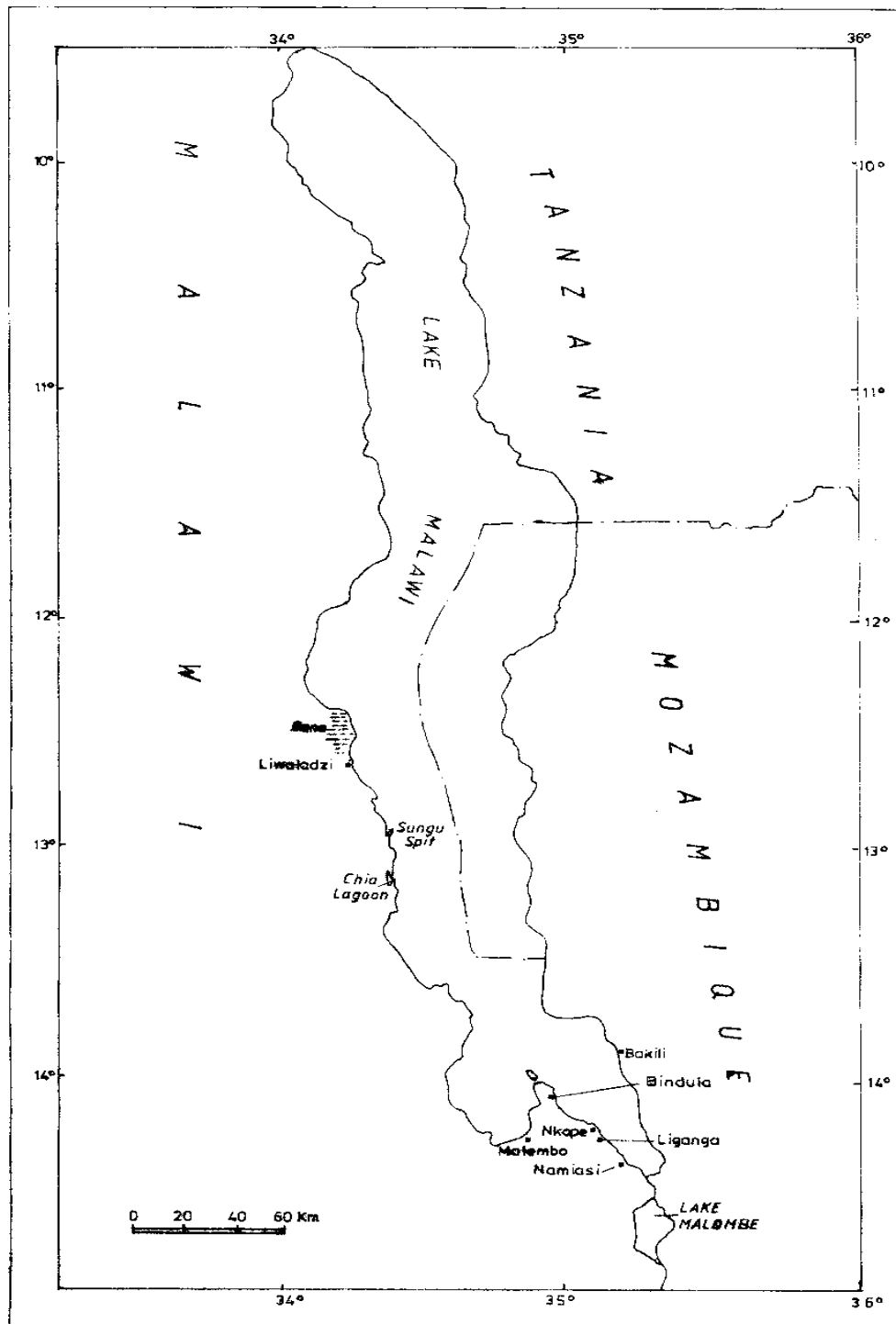


Figure 29: Map of Lake Malawi showing fish landing sites sampled for *Taeniolethrinops praeorbitalis*

Results achieved

A summary of number of alleles showed that all the populations exhibited relatively high allelic diversity (Figure 30) and that there was no significant difference in allelic diversity between Mangochi and Nkhota-kota populations (Figure 31). Observed and expected heterozygosities of Mangochi and Nkhota-kota populations were not significantly different and there was 60% heterozygosity deficiency. A summary of Hardy-Weinberg Equilibrium (HWE) tests indicated that at six loci almost all population showed significant departure from HWE. All pairs of loci were in linkage equilibrium except for UNH130 and UNH 132 locus pair which was in significant linkage disequilibrium. P values from genic differentiation test indicated that each population pair among and between Mangochi and Nkhota-kota populations was significantly differentiated and mean F_{ST} value ($F_{ST} = 0.1517$) showed a population differentiation of 15%. Mantel's test indicated low and insignificant positive correlation between genetic and geographical distance ($Z = 0.06$, $P = 0.65$) and this was concomitant with the MDS analysis results, which showed genetic relationships not corresponding with geographical distance (Figure 32).

Distribution of *T. praeorbitalis* populations seem to cover the whole lake though some areas between Nkhota-kota and Chirumba show no existence of these populations. These populations are more widely distributed in the southern and central parts of the lake. These areas are shallower than the northern part and their shore is mainly sandy. The area between Nkhota-kota and Chirumba has the deepest parts of Lake Malawi and its shore is rocky and deep; therefore it is unlikely that these populations can be found in abundance around this area since this *T. praeorbitalis* is common over open sand in shallow water to the depth of not more than 50 metres.

Populations of *T. praeorbitalis* were not in HWE implying that these populations are violating the assumptions of HWE. The test on number of migrants per generation showed that there were eight individuals migrating between populations each generation suggesting that there is mixing of these populations.

Among the Mangochi and Nkhota-kota populations, there is still considerable amount of genetic diversity as indicated by a good proportion of rare alleles represented by margins between observed and effective number of alleles (Figure 30). Large margin between the two indicates the existence of several low frequency alleles (rare alleles). Although the Mangochi populations generally experience a higher exploitation pressure, their allelic diversity is not significantly different from that of Nkhota-kota populations (Figure 32).

All population pairs were significantly differentiated at the six loci indicating that the populations are still distinct both in Mangochi and Nkhota-kota suggesting considerable population structuring. The amount of differentiation among these populations is 15.2%.

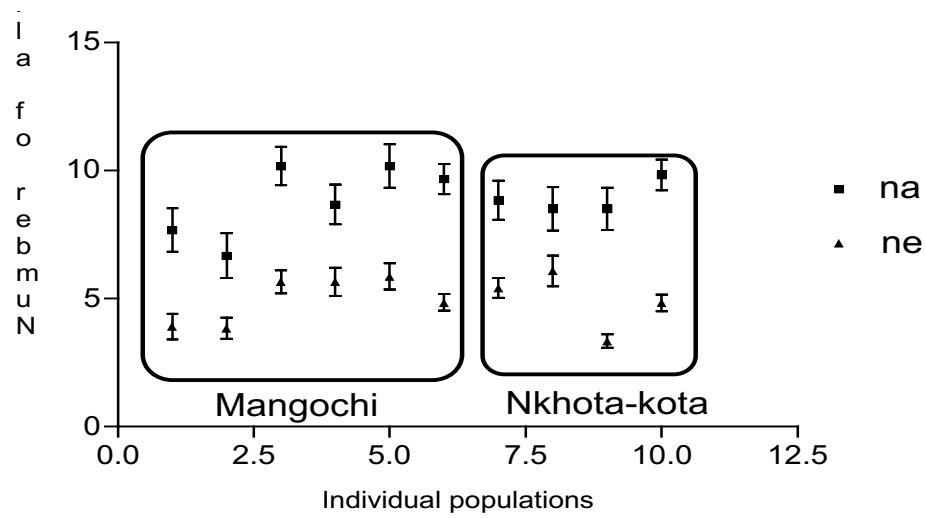


Figure 30. Allelic diversity of sampled populations

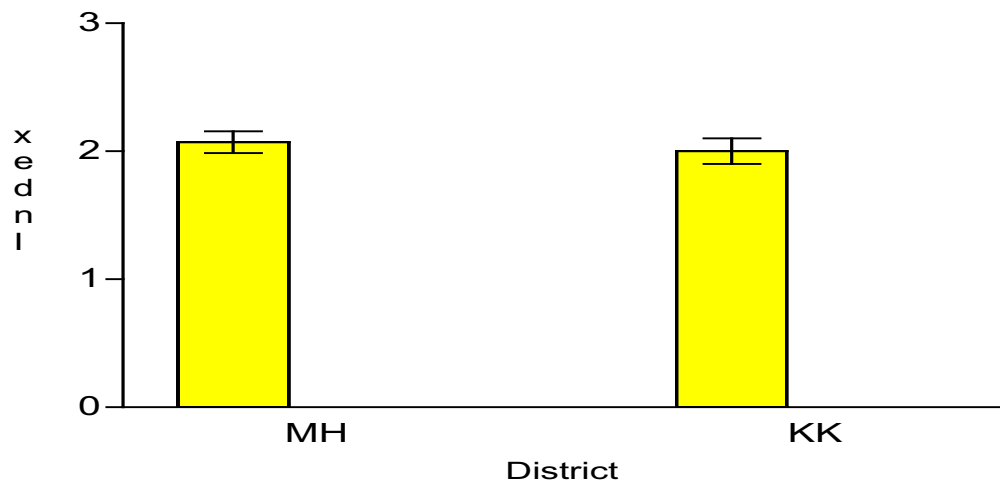


Figure 31. Shannon's Information Index at six loci for pooled Mangochi (MH) and Nkhota-kota (KK) *Taeniolethrinops praeorbitalis* populations.

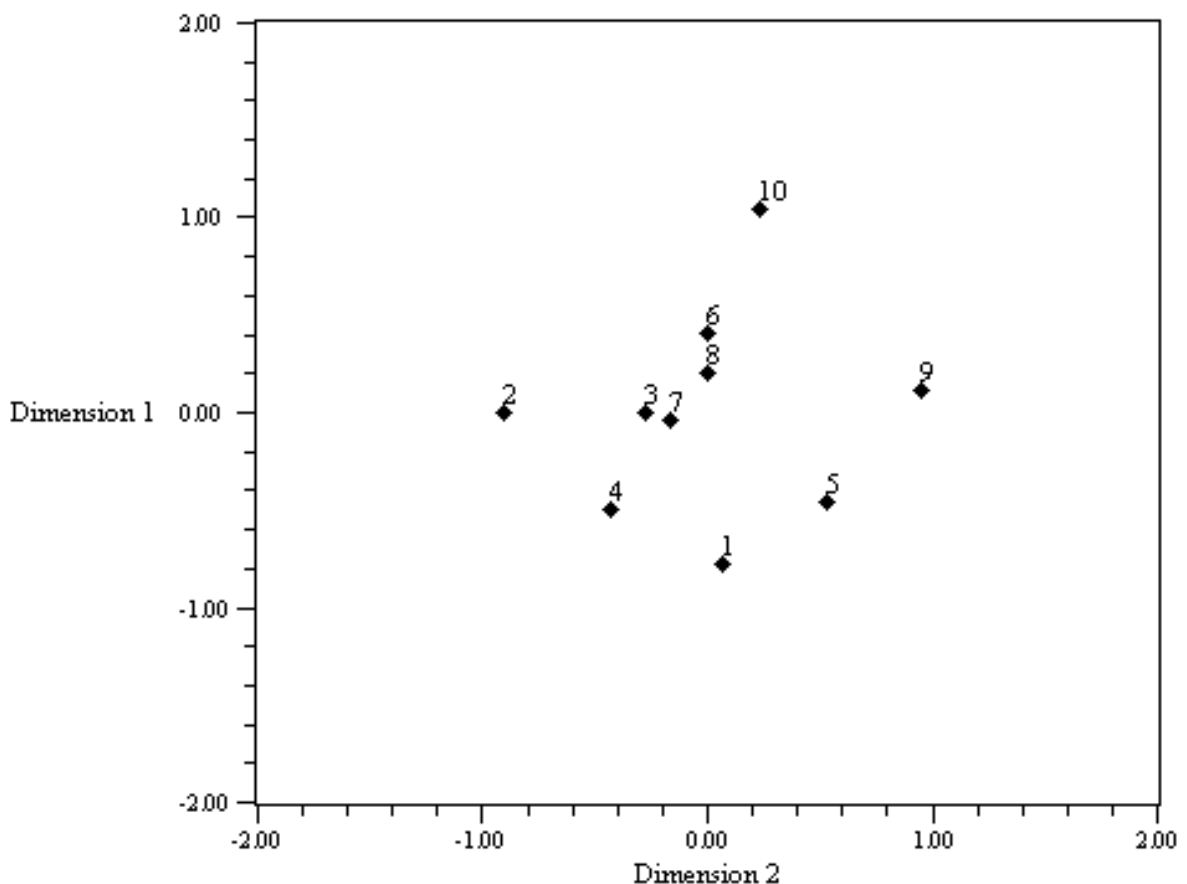


Figure 32. Genetic relationships between populations of *Taeniolethrinops praeorbitalis*. The plot is against dimension 1 and 2 of the configuration produced by multidimensional scaling (MDS) analysis of Nei's Genetic distances. 1-6 (1 Bindula, 2 Malembo 3 Nkope, 4 Liganga 5 Bakili, 6 Namiasi) Mangochi populations and 7-10 (7 Liwaladzi, 8 Chia 9 Bana 10 Sungu Spit) Nkhota-kota populations.

Problems encountered

Several problems were experienced in the course of this work, which included the following:

1. Sample collection did not go as planned because in some fish landing sites, samples would not be found either because by the time we arrived they had all been sold or the catch did not have the species (*T. praeorbitalis*). This meant going to same fishing landing sites more than once. In some cases we had to return to a fish-landing site the next rainy season since more fish are caught during the rainy season.
2. We were also delayed by the slowness of the ABI Genetic Analyser given the fact that at least fifty fish samples were to be analysed per each of the ten sites. The ABI Genetic Analyser using Genescan Programme took 24 minutes to analyse a single sample.

Another delay resulted from late delivery of consumable used for running the genetic analyzer since the suppliers were based in South Africa.

Papers and publications

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Conclusions

In 1999 *T. praeorbitalis* specimen were collected from fish landing docks in Nkhota-kota District, in the central region, and Mangochi district. A summary of number of alleles showed that all the populations exhibited relatively high allelic diversity, with no significant difference in allelic diversity between Mangochi and Nkhota-kota populations. A summary of Hardy-Weinberg Equilibrium (HWE) tests indicated that at six loci almost all population showed significant departure from HWE. A low and insignificant positive correlation between genetic and geographical distance ($Z = 0.06$, $P = 0.65$) concurred with MDS analysis results, which showed genetic relationships not corresponding with geographical distance. Overall, among the Mangochi and Nkhota-kota populations, there is still considerable amount of local genetic diversity, indicated by a good proportion of rare alleles represented by margins between observed and effective number of alleles. Although the Mangochi populations generally experience a higher exploitation pressure, their allelic diversity was not significantly different from that of Nkhota-kota populations.

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Partner 8: Department of Fisheries, Fisheries research Unit (MNRMW.FD.FRL)

Reporting scientist: Dr Moses Banda.

Other contributors: M. M. Manase, Geoffrey Z. Kanyerere

Objectives

The Trophic Ecology of the Demersal Fish Community of Lake Malawi/Niassa, Central Africa, Contract No. ERBIC18CT97-0195, was a regional project involving the riparian countries Malawi, Mozambique and Tanzania, and funded under the European Commission Workprogramme 'Cooperation with Third Countries and International Organisations, Part C: Scientific and Technical Cooperation with Developing Countries.' The project was a four year programme from March 1998 to February 2002 and was launched at Senga Bay, Malawi in March 1998 but the research work began in September of the same year. The Trophic Ecology of the Demersal Fish Community of Lake Malawi/Niassa, Central Africa was basically a follow up project on the stock assessment and exploitation studies of the demersal fish stocks by Banda and Tómasson between 1994-1996, and other previous donor supported programmes such as ODA UK/SADC Project, which lacked in-depth ecological studies and the basis of fish production. The project general objectives of the project were:

- ❑ To formulate trophic models that will quantify energy flows through the demersal fish community and food web that supports it in order to understand the primary components of the food web and detect the main ecological effects of disturbance, such as an increase in fishing activity, on it.
- ❑ To determine the existing fishing pressure on the demersal fish community through analysis of collected statistics in Malawi and Tanzania and evaluate the accuracy of those statistics through calibration studies.
- ❑ To identify, and produce guides for the main species of benthic invertebrates

Six key activities were identified in pursuit of the main objectives as outlined below:

- i. The taxonomic description of main fish and invertebrate components relevant to the demersal fish community.
- ii. The estimation of density, standing biomass estimates, growth and production rates of the main components of the food web at different depths.
- iii. The description of diet and quantification of feeding rates of the main species of demersal fish.
- iv. The determination of catch efficiencies and selectivities of different techniques used to exploit the demersal fish community.
- v. The estimation of fishing and natural mortality of the main demersal fish species. The estimation of the spatial distribution of fishing effort

An integrated research approach was adopted for the project because of its regional nature and the fact that the specific objectives were interlinked. Based on this, 9 project tasks were defined for the successful implementation of the project and included 1) Programme planning & project co-ordination, 2) Primary photosynthetic and microbial production, 3) Invertebrate communities, 4) Zooplankton assessment and *Chaoborus* diet analysis, 5) Fish taxonomy, 6) Fish handbook, 7) Fish stock assessment and growth rates analysis, 8) Fish diet analysis, 9) Stable isotope work, 10) Trophic modelling, and 11) Collation and interpretation of Tasks 2-8. Recognising the fact that integration can only be achieved through partnership, eight partners namely University of Dublin, Trinity College, Ireland, Koninkijk Belgisch Instituut voor Natuurwetenschappen, Belgium, Koninkijk Museum voor Midden-Afrika, Belgium, University of Hull, U.K., University of East Anglia, U.K., University of Southampton, U.K., Chancellor College, University of Malawi, Department of Fisheries, Malawi and Ministry of Tourism, Natural Resources and Environment, Tanzania participated in the implementation of the programme, with the University of Dublin, Trinity College, Ireland as the Project Coordinator. Ministry of Agriculture & Fisheries, Mozambique was an associated scientific partner included in all regional discussions on the research issues as it is a trilateral member while the Global Environmental Facility, Salima, Malawi and Institut für Geologie und Paläontologie, Tübingen, Germany were sub-contractors to the project.

Each project task was assigned to one or more partners who formulated research activities pertaining to the successful accomplishment of such a task. The research activities were discussed and agreed with other partners prior to their implementation.

The primary activities under the EU project consisted of investments in basic research with three principal objectives as follows:

- to assess the impact of gears on the commercial important fish species through the assessment of species and size composition of catches.
- To estimate the biological and population dynamic parameters.
- To assess the spatial distribution of fishing effort.

The principal activities would be achieved through the four research activity components: Traditional gear selectivity surveys, gillnet selectivity surveys, populations parameters, frame survey and trawl selectivity surveys. Each component had specific objectives, which were as follows:

- a) The traditional gear selectivity surveys were designed to assess the performance and selectivity of the traditional gears in terms of size and species composition and also to record their mode of operations. This research activity was a contribution towards the EU Project activity that sought to find out the relative catch efficiencies and selectivity of the different fishing techniques used to exploit the demersal fish community.
- b) The objective of the gillnet selectivity surveys was to establish gillnet selectivity curves in Lake Malawi for the deep water as well as for shallow fishes by examining different legal meshes. The gillnet fishery is the one of the largest fisheries on the lake. This research activity was a contribution towards EU Project activity that sought to find out the relative

catch efficiencies and selectivity of the different fishing techniques used to exploit the demersal fish community.

- c) The objectives of the trawl selectivity surveys were to establish trawl selectivity curves for Lake Malawi demersal trawl fisheries and selection factors for commercially important fish species, and quantify the effect of clogging on the selectivity. This research activity was a contribution towards EU Project activity, which sought to find out the relative catch efficiencies and selectivity of the different fishing techniques used to exploit the demersal fish community.
- d) The main objective of the frame survey was to generate information that can be used to work out the numbers and spatial distribution of fishing effort in terms of fishing crafts, fishing nets, number of fishermen and assistants on Lake Malawi for the traditional fisheries. The information from this activity was a contribution towards EU Project activity, which aimed at estimating the spatial distribution of fishing effort throughout the lake.
- e) The population parameter research activity was designed to assess the status of the important fish stocks of the demersal community by estimating population parameters including growth, sexual maturity, fishing and natural mortality as inputs in the analytical biomass models. This activity was a contribution to EU project activity which sought to estimate the fishing and natural mortality of the main demersal fish species.

The above research activities, which were peer reviewed by the University of Southampton, U.K. formed the research contract no. ERBIC18CT97-0195 (DG 12-CPPE) between the Department of Fisheries and the EU. These research activities were part of the research programmes of the Department of Fisheries and the collected data from such activities were also relevant for use in the EU Project.

Scientific Activity Report

Of the five-project research activities four activities were implemented as follows:

1 Traditional gear selectivity surveys

Lake wide and regular monthly surveys each with a sampling period of 20 and 3 days respectively were conducted between 1998 and 2001. Regular surveys on a monthly basis have been carried out in the southeast arm since 1999 whilst lake wide surveys covered all minor strata of the lake. The lakewide surveys were co-financed by EU and Department of Fisheries whilst the monthly surveys were under the sponsorship of the National Aquatic Resource Management Programme funded by GTZ. Selected landing sites for sampling which fulfilled two basic criteria- different fishing gears, landing and accessibility by road network were chosen based on the routine Catch Assessment Survey inventory along the coastline. The fishing areas of Mangochi, Salima, Nkhatakota, NkhataBay and Karonga were sampled during each survey. Six main fishing gear types chilimira, gillnets, beach seines, nkacha, handlines, longlines and fish traps were sampled per day and depending on the availability of the gears on the beach 1-8 catches were sampled for each gear type. The size of the sub-sample was determined by the size of the catch landed by a particular gear and in most cases

the sub-sample was 10% of the catch. Complete samples were taken for gears that landed with very small catches and less than 10% samples were taken from gears landing large catches of small fish. All catches from each gear type were identified to species level and total weight of each species recorded. Total length of individual fish for each species was also measured. However, due to some identification problems some species were keyed out to genus level such as *Oreochromis* spp.

2 Gillnet selectivity surveys

The gillnet selectivity surveys were initially designed to concentrate in the south east arm of the Lake Malawi the main fishing ground of *Oreochromis* spp. which is the dominant fish species in the gillnet fishery. Bi-monthly sampling surveys were planned for this exercise from the inception of the project to June 2000 and each trip was scheduled for about 5 days. Preliminary results from this study and the above one however, necessitated the inclusion of the central waters in surveys in order to capture new developments arising in the fisheries during the project period. The surveys were then rescheduled to monthly sampling to last for 10 days from July 2000 to March 2002. Two sites were sampled in the southeast arm of the lake, one on the eastern side and the other on the western side. In contrast, four sites were sampled in the central waters and all were on the western part of the lake. Samples were collected from gillnets of variable mesh sizes which happen to land at selected site and the choice of the site was dependant on the availability of the fishers. The sampling sites varied from one survey to another or within each sampling period because the gill-netters are so mobile. A minimum of ten gillnets were sampled at each sampling site. The catch was keyed to species composition and the total weight of each species recorded. The length and body depth of individual fish was then measured. The mesh size of each sampled gear was also recorded. EU and the Department of Fisheries were the co-financiers of this exercise.

3 Trawl selectivity studies

Trawl selectivity surveys were conducted in the deep waters > 50 m of south east of Lake Malawi employing 2 combinations of two types of codends. The first combinations comprised two codends, stretch mesh size 38 mm and 50 mm, and the other one the two codends, stretch mesh 50 mm and 100 mm. The research vessel Ndunduma, powered by a caterpillar engine of 386 hp, collected the data. A Gulloppur bottom trawl net was used with a head rope of 23 m and a vertical opening of about 4 m was towed at an average speed of 3.5 kn. The codend mesh size was 38 mm. The EU and the Department of Fisheries funded the surveys.

4 Frame Survey

Frame Survey is an annual event and involves a complete census of basic fishing units and fishers. During the duration of the project, Frame Survey visits to all landing sites along the shore involved counting fishermen, their gears and fishing crafts and it was jointly funded by Department of Fisheries, Natural Resource Management Aquatic Programme (NARMAP) under GTZ funding and the Icelandic International Development Agency (ICEIDA).

Results Achieved

1 Traditional gear selectivity surveys

Six lake wide surveys out of the 12 planned surveys were conducted between 1998 and 2001 while all regular monthly surveys were conducted as scheduled. Because of the small sample sizes in various sampling sites the data was analysed with reference to catch composition only. A total of 178 fish species/groups were identified during the surveys. Species diversity was dependant on mesh sizes and diversity was high in small meshed gears. There was also an apparent high degree of species overlap in gear catches, which is perhaps attributable to multi-species nature of the fisheries. *Copadichromis virginalis* locally known, as 'utaka' was the dominant species commonly caught in all sampling areas. The presence of some demersal deep species such as *Alticorpus geoffreyi*, *A. mentale*, *Lethrinops gossei*, *L. alba* and *Placisochromis tokoloshi* especially in the gillnet fishery and chilimira suggest that the artisanal fisheries are not only confined to inshore areas. All the five species are deep-water species found in waters >50 m depth.

The sample size for different gears was variable (Table 29). The modification of some gears and the fishing pattern developed by intuitive fishers in the last few years or so was noted during this survey. Gillnets in most areas for instance are no longer passive gears as traditionally believed. Most gillnets are dragged like beach or open water seines and have an illegal mesh size < 2-inches that target *C. virginalis* which is mostly caught using the open water seines (Chilimira). Some bottom set gillnets had hooks fixed on the foot and head ropes. In stand alone situations, fishers beat the waters around the set gillnets or the canoe with the intention of driving the fish towards the gear. This shifting tendency of the fishers from large meshes to small meshed gillnets signifies the declining catches attributable to declining of large fish species like *Oreochromis* spp. This in turn results in reduction of revenue since the fishery targets the less economic value fish species.

Table 29. Number of gears sampled in each major stratum during various surveys undertaken between December 1998 and December 1999.

Major stratum	BS	CH	GN1	GN2	GN3	LL	HL	Nk
2	19	77	59	7	86	6	30	23
3	4	28	1	4	2	1	9	
4		39	2	3	7		2	
5	6	24	17	2	10	1	6	
6	4	18	6	5	1	1	7	
7	1	38	21	14	8	4	7	

In light attraction fishery of the chilimira especially in the southeast arm of the lake, the adoption of the new fishing pattern had positive results. Historically, light attraction fisheries have always mainly targeted the cyprinid sardine like fish, *Engraulicypris sardella*. Recently, however, the modification of the gear and fishing methodology have targeted *Oreochromis* spp. one of the highly priced fish in the lake, which dominated the catches of gillnets and chambo beach seines in the last decade. Catch composition of all gears sampled was multi-species and a total of 178 fish species were identified in the small-scale fishery during the surveys (Table 30).

Table 30. Total number of fish species identified in each gear type and in each sampling area during catch composition surveys of the small-scale fishery between September 1998 and January 2000 in Lake Malawi.

Gear Type	No. of species	Area	No. of Species
Beach seines	89	SE Arm	160
Chilimira nets	142	SW Arm	95
GN1 Gill nets	136	Salima	83
GN2 Gill nets	96	Nkhotakota	132
GN3 Gill nets	75	Nkhata Bay	80
GN4 Gill nets	8	Karonga	136
Hand lines	88	All areas	178
Longlines	9		
Nkacha nets	61		

2 Gillnet selectivity survey

Fourteen gillnet selectivity surveys that account for 42% of the planned surveys during the life span of the project were done. Six surveys were done between 1998 and June 2000 and the rest from July 2000 to project completion time. The data collected from the south east of Lake Malawi form the basis for the gillnet report while that from the central waters supplemented that of the Traditional Gear Selectivity studies as the sample size was small. Over 120 fish species/groups were recorded in this study and the size selectivity of some important commercial fish species was estimated. The catch of the small meshed gillnets was dominated mostly by small fish species of the genera *Copadichromis* (74%), *Lethrinops* (4%), *Synodontis* (3%), *Otopharynx* (2%) and *Aulonocara* (2%), which contributed over 84% of the total catch. The small individuals of the catfish genus *Bagrus* accounted for about 6% of the total catch and the rest was for other fish species. The large fish species of the genera *Oreochromis* (70%), *Bagrus* (10 %), *Bathyclarias* (8%), *Barbus* (6%) and *Buccochromis* (2%) dominated catches of gillnets of mesh sizes > 3-inches. The small meshed gillnets have the potential to catch the immature *Oreochromis* spp. but its absence in the corresponding catch suggests that they are set in deep waters out of their reach. The presence of immature catfish of *Bagrus* vindicates this.

3 Trawl selectivity

One survey employing two codends of stretch mesh size 38 mm and 50 mm was carried out and the gear selection ogives, selection factors and the length at 50% retention for *Diplotaxodon elongate*, *L. oliveri*, *L. alta* and *L. gossie* were established for both codends. A comparison of the 50% retention length to 50% maturity length of these species indicates that all species were mostly caught before they reach maturity. The clogging rate for both nets was within 15 minutes after commencement of trawling. These results indicate clearly that the present recommended mesh size is destructive to the demersal stocks of Lake Malawi.

4 Frame survey

One frame survey was carried out in August 1999 during the dry season when most landing sites were accessible by land. The Frame Survey results indicated that the number of fishermen, fishing gears (in particular small mesh gears) and vessels has increased enormously in almost all the districts. For some gears, such as gillnets, the increase has been accompanied by a decline in mesh size.

Problems encountered

Financial resources were the main constraints that affected the successful completion of the research activities. During the onset of the project it was agreed between the EU and Department of Fisheries that the joint project research activities will be co-financed by the two partners. A series of surveys at the commencement of the project between 1998 and June 1999 were funded using monies from a revolving fund of the Department of Fisheries while awaiting the EU fund injection. The ongoing changes in Government financial management transactions, which started in the 1999-2000 financial year, affected the operation of the fund resulting in the inconsistent availability of the funds for research activities. The inconsistent availability of funds disrupted the research activities implementing schedule under this source, which further led to delay in implementation or cancellation of the research activities.

The first EU fund injection to the Department of Fisheries for the agreed research activities was made towards the end of 1998 after the foreign account in Malawi was established. The funds however, were made available to the implementing agent, Fisheries Research Unit (FRU), until June 1999. Some administrative logistics hindered the flow of money from the Foreign Account to FRU, which meant that the research activities during this period were funded from Department of Fisheries financial resources. FRU opened an operational account in Mangochi to facilitate the smooth implementation of the project activities after the resolution of the existing problems. Two transfers were effected between June and August 1999 from the foreign account to the operational account and the transferred monies covered the costs of two research surveys, the traditional gear and gillnet selectivity surveys. The remaining balance in the operational account was insufficient to meet the budget of any research activity. There was also no money in the foreign account apart from the operational balance. The operational modus operandi of the foreign accounts entails the maintenance of a certain minimum balance in the account. Accessibility to additional EU funds by the Department of Fisheries was not possible because the EU funding procedure is based on reimbursement, which is only feasible when the initial deposit for the activities is spent and properly accounted for. Unfortunately, the Department of Fisheries could not account for the initial deposit because of the inaccessible balance in the foreign accounts.

A third transfer was made in December 1999 after lengthy negotiations with the bank to reduce the balance to almost half of the original. These funds with the balance in the operating account from the initial transfers covered the cost of two research activities, the traditional gear and gillnet selectivity surveys. The cost statement was sent in view of the above costs but reimbursement was not possible because of the funds in the foreign account. Accessibility to the balance would have led to the closure of the foreign account thereby defeating the initial objectives of the account. The establishment of this foreign account was also problematic. Therefore, the Department of Fisheries was in a dilemma and maintained the account at the expense of the project activities implementation. The shortage of funds compounded the situation. If there were enough funds to the equivalent of the balance in the bank at any other time the Department of Fisheries would have used such monies to offset the balance and then submit the claim. However, the Department of Fisheries closed the account early 2002 and used the funds for the intended purpose. Because of the failure of the Department of Fisheries to reclaim monies from EU in time most of the

activities have been funded using its resources and the implementation of such activities depended on the resources available.

Technology implementation plan

The findings of the four research activities satisfy not only the EU project objectives, but also serve the mandate of research in the Department of Fisheries. All the results are inputs in the formulation process of the management strategy at gear selectivity and utilisation levels as depicted in the flow chart in section 1.3. The formulation of a Lake Malawi management strategy is a long-term activity that will take time and needs adequate financial resources and probably no single strategy will be appropriate for the lake, because of different fisheries characteristics in different areas. Therefore, it is only logical to divide the lake into management zones/units depending on the biological trait and each zone should have a management plan. The creation of such management zones is underway in the southeast arm of Lake Malawi based on the fact that it is the main fishing ground of the most valued fish in Malawi, *Oreochromis* spp. which is on the decline. The proposed area is a vast expanse of shallow water with a maximum depth of <40 m. The formulation of management recommendations based on the results emerging from some of these studies are also underway. While this process may take sometime the results from gillnet selectivity studies and Frame Surveys will be used in the amendment of the fisheries management regulations after being discussed with stakeholders during the resource management workshop scheduled for June 2003, the end of this fiscal year. Most gillnets have illegal mesh size and fishing effort is very high which is unsustainable for some fish stocks such as *Oreochromis* spp. The Frame Survey findings in conjunction with monthly catch and effort data are still used for the estimation of the total fish landings. No Frame Survey has been carried out since 1999 except in Mangochi area. All this information forms the basis for the formulation of the management plan and definitely some recommendations emanating from these studies will be adopted in the management plan for the southeast arm of the lake.

Publications and papers

- Kanyerere, G.Z. 1999. Trawl selectivity and effect of clogging on selectivity in standard trawl surveys in Lake Malawi. Fisheries Bulletin N0. 39. Fisheries Department, Lilongwe, Malawi.
- Weyl, O.L.F, Banda, M., Sodzapanja, G., Mwenekibombwe, L.H., Namoto, W., and Mponda, O.C. 2000. Annual Frame Survey September 1999. Fisheries Bulletin No. 42. Fisheries Department, Lilongwe, Malawi.
- Sipawe, R.D. 2001. Gear and species selectivity in the gillnet fishery in Lake Malawi. Proceedings of the Lake Malawi Fisheries Management Symposium, 4-9th 2001, Capital Hotel, Lilongwe, Malawi. In: (Eds.) O.L.F. Weyl & M.V. Weyl, pp133-141.
- Manase, M. 2002. Malawi's small-scale Fishery Gear selectivity and performance in lake Malawi. Fisheries Bulletin No. (in press). Fisheries Department, Lilongwe, Malawi.

The trawl net selectivity studies and the Frame survey results have been published in Department of Fisheries internal publications as Fisheries Bulletin 39 and 42, respectively. The gillnet selectivity studies have been published as proceedings of the Lake Malawi Fisheries Management Symposium which took place in 20001 in

Malawi. The traditional gear selectivity survey is in press and will be published as the Fisheries Bulletin.

Conclusion

The fisheries of Lake Malawi are multi-species as indicated by the selectivity studies which confirm that single species models that have been employed in the management of the demersal fisheries are inappropriate, which allow the exploitation of one fish stock at the expense of the other. Management strategies based on the holistic approach may provide effective management of the fisheries resources on the lake.

The studies show that most fishing gears in the artisanal fisheries on the lake are illegal because they do not have the legally prescribed mesh size. There has been a shift in mesh sizes from large to small meshes for most gears, which in most cases is caused by decline of large fish in the fisheries. The small mesh gears pose a threat to biodiversity because of the high species diversity in the catch composition. They also catch small immature fish of large species and both growth and recruitment overfishing are imminent with high fishing pressure caused by increasing effort as depicted from the Frame Survey data. Localised overfishing is becoming a common phenomenon in the traditional fisheries of Lake Malawi. The shift in mesh sizes of the gears has also been accompanied by modifications of gears and fishing techniques, which are also ascribed to the declining of the large fishes.

The legal prescribed mesh size for trawler nets is 38 mm and the review based on the trawl selectivity studies indicate that the 38 mm mesh sizes clog within 15 minutes and yet the average minimum trawling duration is about 120 minutes. Most of the fish caught are also immature. In practise therefore the trawl fishery has no mesh size regulations and also pose a threat to biodiversity.

The presence of some deep-water species in the artisanal gears is manifest that the fishery is tapping the offshore deep fish resources. The current experience from experimental trawl fishing supports this. Trawling on the north eastern side of the southeast arm is not easy currently because of the numerous illegal day setting gillnets from 40 to 80 m water deep. The owners of these gears guard them, making trawling in the midst of fishers almost impossible. Open water seines exploit fish in waters < 40 m deep while gillnets are set in waters of > 40 m deep probably to avoid social conflicts. This fishing pattern entails that bottom trawling is confined to waters greater than > 80 m.

The integration of the findings strongly indicates that the southeast arm where most of the work was based is under severe fishing pressure that requires sustainable management strategies to be placed immediately to minimise further environmental deterioration. Virtually all the depth ranges seem to be exploited at present as vindicated by these research activities. There is a proliferation of small meshed gear fisheries in the area, which is extremely destructive to the fisheries resources and the mode of their operations also accelerates environmental degradation.

In view of the rapid change in gear pattern utilisation, general increase in fishing effort, the fast decline of economical value species with no signs of rebuilding and the absence of effective management strategies, the Government priority area should be the conduction regular monitoring surveys to address the changes taking place in the

fishery. The selectivity research activities can be considered as complementary monitoring surveys of the artisanal fisheries, which have often been neglected due to the complex nature of the fisheries. The artisanal fisheries have been monitored through Catch and Effort Surveys which has short falls in terms of accuracy and the fact that the analysis of the data lags behind, because of some administrative logistic problems in the collection of the data from various districts. CAS tends to provide meaningful results if it is up to date and does not show the biological impact of fishing on the fish stocks. It is therefore recommended that the long-term research studies established through the EU initiative should continue to be part of the monitoring programme for the artisanal fisheries. The studies will give information on the changes taking place in different fisheries thereby providing useful input in the formulation of the management strategies of the lake. Due to financial resources constraints, bi-annual traditional selectivity studies are recommended on a regular basis.

Partner 9: Tanzanian Fisheries Research Institute (TANZ.FRI)

Reporting Scientist: Dr Benjamin Ngatunga

Objectives

Objectives of TANZ.FRI were to conduct a survey of the artisanal fisheries in the Tanzanian sector of Lake Malawi/Nyasa and to provide training for fish taxonomy (identification) at the Kyela Research centre.

The overall objectives of the work were:

- The catch assessment survey of the artisanal fisheries in the Tanzanian sector of Lake Malawi/Nyasa.
- Training of fish taxonomy (identification) to a number of Tanzanian Fisheries working directly in the field and involved in statistical data collection or extension work.
- The Fisheries Frame Survey

Scientific Activity Report

Part 1: Catch Assessment Survey

It is not known when the last survey was conducted in the Tanzanian waters of Lake Nyasa and basic information on number of fisherman, nature and extent of gears and total catch did not exist prior to the work of the project. The survey was designed to cover the whole of Tanzanian territorial waters, stretching from the border with Malawi (Kyela district) to the border with Mozambique (Mbinga district). The approach is to conduct a complete enumeration of all the landing sites, fishermen, fishing vessels and fishing gears by type and size.

This Artisanal fisheries survey in the Tanzanian side of the lake was part of the lake-wide survey aimed at estimating fishing activities throughout the lake. In Tanzania this survey was a one year programme which ended in March 2000. The primary

objective of the survey was to obtain reliable current estimates for the Tanzanian side of Lake Nyasa of the total quantity of fish harvested by the fishermen from the lake (in terms of live weight in tons). Secondary objectives included knowing the species composition of the catch and the fishing effort involved in obtaining the catch.

The programme involved selection of six landing site otherwise referred to as primary sampling units (Kiwira, Matema, Lupingu, Manda, Liuli and Mbamba Bay), selection and training of beach recorders one for each landing site. At each of the selected sites and for each month the recorder was to identify and record the distribution of gear type, determine the average total catch for each gear type and allocate the sampling effort across gear types to reflect the relative proportion of each fish catch taken in the area. For example if the combined catch for gillnets is the largest of all the gears then gillnets should be sampled the most intensively.

Each gear, was sampled regularly and the following data was obtained:

- Total Catch weight
- Catch composition (identifiable species/species groups/commercial/groups).
- Length frequency distributions (only when identification to species was possible).
- Collection of fish samples (for dominant species groups).

Each gear was sampled minimum three times each month and included Full Moon, Half Moon and No Moon.

The data collected during this survey was designed to, not only allow for direct comparisons between the fisheries of each country, but also for use as a comparative set of data for assessing the efficacy of the current assessment system in Tanzania. Parallel surveys were also supposed to be conducted in the Malawi and Mozambique sectors of the lake. The data was also supposed to reveal the artisanal fish production from the lake, a figure required for input in the benthic ecosystem trophic model.

Part 2: Taxonomy training

The specific objective of this training were:

- To standardize the taxonomy of the commercially important fish species throughout the lake. Before this training only the taxonomic records from the Malawian side were up to-date. For example old generic name of Cyprinid *Barilius* was still in use in Tanzania and Mozambique instead of the new generic name *Opsaridium*. Likewise the use of generic names *Haplochromis* and *Tilapia* were still not updated. There were a lot of sex confusion where scientific names were compared in the three riparian states.
- To create awareness of the ichthyodiversity of Lake Nyasa in the light of conservation, consumptive and non-consumptive utilization of the fish resources. Participants in the training were made aware of the rich ichthyodiversity of the lake and how the resource can be availed for economic benefit of the country through direct consumption and ecotourism. Before this training most of the Tanzanian did not know the potentiality of the lake as

a tourist paradise. That the lake contains the highest number of freshwater fish species in the world most of which are only in Lake Nyasa basin.

- To make sure that taxonomic knowledge is passed on to others. There are very few people who can identify Lake Nyasa fishes with confidence. Most of the people can identify fish using local knowledge but few know the reality about Lake Nyasa fish. Different fish look so similar and similar fish look so different. What is required is a little bit of taxonomic instinct to be exact in identification of the Lake Nyasa fish.

Part 3: Fisheries Frame survey

According to information from the district fisheries authorities from Kyela, Ludewa and Mbinga, the last survey was conducted in the Tanzanian waters of Lake Nyasa in 1970s, but there is some uncertainty as to exact details. Fisheries Frame surveys in Malawi waters of Lake Nyasa are conducted biannually. Under the EU project on the Lake Malawi/Nyasa Trophic Ecology of Demersal Fish Community, Artisanal Fisheries component for the three riparian countries, one of the objectives is to carry out a survey of the Lake Nyasa fisheries in order to assess the current techniques in use, the landing sites the number of fishermen and their catch. It was felt, from the beginning of the project that, these objectives could not be achieved without conducting an organised frame survey for the lake fisheries. However, due to logistics, each riparian state was mandated to conduct the frame survey separately. In Tanzania, the EU funded Artisanal Fisheries Project for Lake Nyasa is being supervised by Prof. P.O.J. Bwathondi, Director General of the Tanzania Fisheries Research Institute and executed by scientist from Kyela Research Centre. This report presents the results of the frame surveys conducted in the three districts of Kyela, Ludewa and Mbinga on the Tanzanian waters of Lake Nyasa. One survey covered the dry season and the other one was conducted during wet season because fishing activity is more intensified during rainy months.

The specific object of the fisheries frame survey were:

- To establish the number of fish landing sites on the lake, determine the number of fishermen, fishing vessels and number of fishing vessels by type and size.
- To estimate the productive potential of the fish stocks in Tanzanian sector of the lake and to determine and recommend sustainable levels of utilization.
- To identify opportunities and technical requirements for increasing fish production.

The survey covered the three districts of Kyela (Mbeya region), Ludewa (Iringa region) and Mbinga (Ruvuma region), stretching from the border with Malawi (Songwe river) to the border with Mozambique. Each district has two divisions namely Ntshela and Nvakvusa (in Kyela) Mwambao and Masasi (in Ludewa) and

Ruhuhu and Luhekei (in Mbinga). A total of twenty six fishing location were identified each with a minimum of one and maximum of four landing sites. (Figure 33). The approach was to conduct a complete enumeration of all the landing sites, fishermen, fishing vessels and fishing gears by type and size. Due to topography of the lake and to unaccessibility of some parts of the lakeshores by road, water transport (by boat) was the most appropriate approach with the aim of covering the whole Tanzanian coastline.

A questionnaire was adopted from the one in use in the other Tanzanian lakes and just modified to suit the situation in Lake Nyasa. All information was entered in purposely designed data forms. Twotypes of forms were used:

- Form A – to record details of the number of craft on landing site and facilities that are to be found in each landing and other infrastructure like road and nearest market.
- Form B – to record details of each fishing craft (ignoring transport craft) and fishing gear in use in each craft.

The approach was to conduct a complete enumeration of all the major landing sites, fishermen, fishing vessels and fishing gears by type and size. Facilities (e.g. infrastructure like buildings, all weather roads etc; boat and net repair and electricity supply) present at the landing were also recorded. Additional information included fisheries department staffing and the nearest market to the landing site

Before conducting the first survey, a team of scientists from TAFIRI – Kyela went around to identify staff and fishermen who would participate in information gathering (enumerators). The objective was to have at least one enumerator for each location. Eight enumerators were identified and trained for two days on how to gather the information required. This training was conducted at the Kyela research centre (for Kyela district), Lupingu and Manda (for Ludewa district) and Liuli and Mbamba bay (for Mbinga). The actual survey took place after the training of the enumerators and lasted for a maximum of five days in order to avoid movement of fishermen between locations.

Past experience has shown that recruiting recorders from among the fishermen themselves increases accuracy and reduces bias (Ngatunga et al, 1999). All the enumerators recruited had the basic secondary education and above, as such they could understand well the forms supplied. There was a beach chairman at each landing site from whom the enumerator could get the necessary information including the number of fishers in the village and the type of gears they use. After such information the enumerators went to the field to verify and physically count them adding any additional observation. One enumerator was to cover one location, giving a total of 26 enumerators for all the three districts.

Results Achieved.

The results of the first frame survey (Tables 31-3) provide a summary of the results of the frame survey from the three districts (Kyela district, Ludewa and Mbinga). Table 34 gives the comparison of the survey results for the three districts.

The shoreline of Lake Nyasa can conveniently be described in the following main ecological zones:-

- rocky habitat of the north-east shoreline (Livingstone mountains).
- wide sandy beaches (Matema, Lupingu, Manda, Mbamba Bay).
- river estuaries associated with swampy areas (Wissman Bay & Amelia Bay).

Fishing activities are mainly artisanal because of the following reasons

- Fishing is by use of dugout canoes only
- Tanzania is on the deeper part of the lake
- The lake ultra-oligotrophic (nutrient poor)
- The lake is very rough and the winds are unpredictable

Fish Exploitation involves five categories of fish communities/habitats are exploited for food and aquarium/ornamental purposes.

1. The rocky shore species comprise mainly two forms: the rock-frequenting categories which are utilized for aquarium purposes and the dwarf form of *Opsaridium* which is believed to be breeding in the lake and never enter the rivers for spawning. At present the rock - frequenting cichlids are not threatened but there is reason for concern about the increasing rate of siltation which cover the algae layer on the rock upon which the fish feed. The second concern is about the uncontrolled aquarium fish trade.

2. The sandy shore species comprise the benthic cichlids that feed and breed on sand. These fish have been heavily affected by beach seining and siltation. The ban of beach seines has been successfully observed in Mbinga district and partly in Ludewa district. Kyela district has been notorious in observing the ban on beach seines as a result most of the inshore cichlids have declined in numbers and size.

3. The Riverine species, mostly cyprinids that run up rivers to spawn. Fishermen have for long time utilized the behaviour of this species to exploit them. Because of the method used to exploit this riverine species, the population of species of *Opsaridium* species has declined to the extend that in recent years, the fishery of *Opsaridium microcephalus* has been the lowest in history. Urgent measures should be sort if stocks of *Opsaridium* species are to be restored to sustainable levels. These measures include a complete ban of fishing around river mouth. Further measures included a study to determine whether the *Opsaridium* stocks in the different rivers are genetically distinct.

4. The pelagic stocks, which are generally under utilized and effort should be made to move the fishery in Lake Nyasa to being mainly offshore in order to exploit this resource.

5. The deeper/benthic water. As in the case of the pelagic stocks, the deep/benthic fish communities are also under-utilized.

Fishing crafts and gears

Fishing is mainly by of dugout canoes (3-7.5m) which are small and unstable - restricted to 2km within the shoreline. The gears in use are gillnets, open-water seines, hook & lines, scoopnets and traps (rare). Catch composition by gear is:

Gillnets: haplochromines, tilapiines, *Opsaridium* spp, *Clarias* sp., and *Bathyclarias* spp and *Bagrus meridionalis*.

Open-water seines: *Engraulicypris sardella*, *Rhamphochromis* spp, *Diplotaxodon* spp, *Copadichromis* spp and *Oreochromis* spp.

Hook & line: *Rhamphochromis* spp, *Clarias* sp, *Bathyclarias* spp, *Bagrus*, *Buccochromis* spp, *Serranochromis robustus* and *Diplotaxodon* spp.

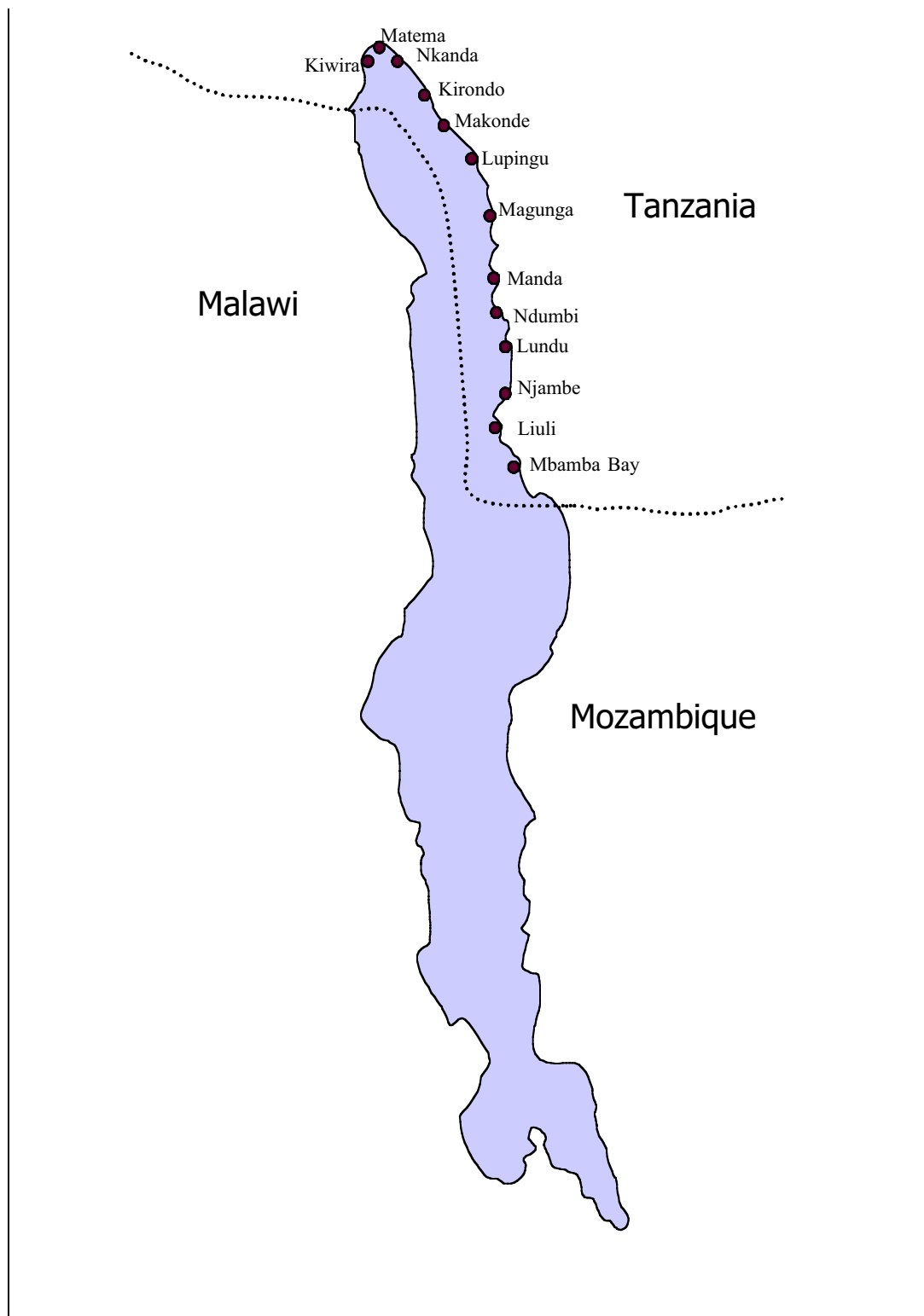


Figure 33: Major fishing communities/villages along the Tanzanian coast of Lake Nyasa

Table 31: Summary of the results for the Kyela district fisheries frame survey (EK1-EK8 = Enumerators).

Item	EK1	EK2	EK3	EK4	EK5	EK6	EK7	EK8	Total
Number of landing sites	4	4	3	3	3	2	3	3	25
Number of fishermen	131	162	125	109	173	79	117	104	1000
Number of fishing vessels	151	148	42	57	138	59	84	87	766
Number of outboard engines	0	0	0	0	0	0	0	0	0
Number of inboard engines	0	0	0	0	0	0	0	0	0
Gears by type:									
Gillnets: <1.5	0	0	0	0	0	0	0	0	0
Gillnets: 1.5	0	7	0	4	0	0	36	157	204
Gillnets: 2.0	312	23	2	9	18	4	89	149	604
Gillnets: 2.5	0	52	3	20	86	72	133	155	485
Gillnets: 3.0	3	31	35	47	105	48	73	73	391
Gillnets: 3.5	0	9	6	22	126	0	164	57	384
Gillnets: 4.0	37	11	0	22	12	0	58	18	158
Gillnets: 4.5	38	54	5	13	4	0	33	89	236
Gillnets: 5.0	0	40	45	29	692	112	31	289	1182
Gillnets: 5.5	0	0	6	0	0	0	2	0	8
Gillnets: 6.0	0	0	0	0	0	88	0	0	44
Gillnets: 6.5	0	0	0	0	0	0	0	0	0
Gillnets: 7.0	0	0	0	0	0	0	0	0	0
Gillnets:>7.0	0	0	0	0	0	0	0	0	0
Total gillnets	390	227	102	166	1043	324	619	987	3696
Long line hooks	0	7981	405	705	700	0	2089	2289	14169
Beach seines	0	1	3	0	0	0	2	0	6
Open water seines	5	38	0	15	18	10	1	5	92
Hand line hooks	1	0	0	3	0	2	0	0	6
Open water Dagaa seines	3	23	7	15	16	6	4	2	76
Mosquito nets	0	4	8	0	1	2	4	0	19
Number of traps	5	0	11	4	22	0	190	25	257
Other (unspecified)	0	0	0	0	0	0	0	0	0

EK1 = Ikombe, EK2 = Matema, EK3 = Mwaya I, EK4 = Mwaya II, EK5 = Itungi port EK6 = Kiwira, EK7 = Songwe I and EK8 = Songwe II

Table 32: Summary of the results for the Ludewa district fisheries frame survey (EL1-EL9 = Enumerators).

Item/Enumerator	EL1	EL2	EL3	EL4	EL5	EL6	EL7	EL8	EL9	Total
Number of landing sites	5	3	3	3	3	3	3	2	3	28
Number of fishermen	116	146	98	205	276	94	124	104	154	1317
Number of fishing vessels	104	104	85	135	176	69	84	53	87	897
Number of outboard engines	0	0	0	0	0	0	0	0	0	0
Number of inboard engines	0	0	0	0	0	0	0	0	0	0
Gears by type:										
Gillnets: <1.5	0	0	0	0	0	0	0	12	14	26
Gillnets: 1.5	0	17	20	30	16	0	10	48	0	141
Gillnets: 2.0	271	133	71	376	26	172	90	52	16	1207
Gillnets: 2.5	235	387	105	280	256	351	345	30	81	2070
Gillnets: 3.0	59	79	24	14	99	10	42	60	159	546
Gillnets: 3.5	35	70	28	0	10	10	67	0	0	220
Gillnets: 4.0	172	214	26	72	161	75	102	24	0	846
Gillnets: 4.5	217	34	13	0	4	6	49	0	0	323
Gillnets: 5.0	49	170	114	67	76	13	38	0	101	628
Gillnets: 5.5	0	12	0	0	0	0	0	0	3	15
Gillnets: 6.0	7	31	6	73	45	18	10	0	134	324
Gillnets: 6.5	0	0	0	3	0	0	0	0	0	3
Gillnets: 7.0	0	1	3	0	14	6	31	0	0	55
Gillnets: 7.5	0	0	0	0	0	0	0	0	0	0
Gillnets: 8.0	0	0	0	6	10	6	117	0	0	139
Gillnets: >8.0	0	0	0	0	0	2	9	0	0	11
Total gillnets	1040	1148	410	921	717	669	910	226	508	6549
Long line hooks	2293	1324	1745	2300	2455	1287	2625	380	700	15109
Beach seines	0	2	10	0	0	0	0	0	4	16
Open water seines	55	48	32	25	56	18	12	3	18	267
Hand line hooks	4	30	3	1	15	1	3	22	3	82
Open water Dagaa seines	0	7	16	36	51	13	10	0	11	144
Mosquito nets	5	2	0	0	0	0	0	0	5	12
Number of traps	0	12	0	0	0	1	0	0	1	14
Other (unspecified)	0	0	0	0	0	0	0	0	0	0

Table 33: Summary of the results for the Mbinga district fisheries frame survey (EM1-EM9 = Enumerators).

Item/Enumerator	EM1	EM2	EM3	EM4	EM5	EM6	EM7	
Number of landing sites	3	4	3	3	4	2	2	
Number of fishermen	447	329	206	181	260	663	459	
Number of fishing vessels	253	183	103	95	154	264	48	
Number of outboard engines	0	0	0	0	0	4D	0	
Number of inboard engines	0	0	0	0	0	0	0	
Gears by type:								
Gillnets: <1.5"	114	0	216	0	0	0	0	
Gillnets: 1.5"	448	841	240	44	1048	0	0	
Gillnets: 2.0"	125	799	130	180	910	495	645	
Gillnets: 2.5"	1061	4457	172	0	196	53	174	
Gillnets: 3.0"	561	2896	126	25	481	204	371	
Gillnets: 3.5"	51	914	0	0	36	239	147	
Gillnets: 4.0"	116	106	298	5	46	376	89	
Gillnets: 4.5"	49	0	0	0	0	79	0	
Gillnets: 5.0"	147	0	0	289	0	28	0	
Gillnets: 5.5"	6	0	0	0	0	0	0	
Gillnets: 6.0"	90	0	0	0	16	0	0	
Gillnets: 6.5"	0	0	0	0	0	0	0	
Gillnets: 7.0"	0	0	0	0	0	0	0	
Gillnets: 7.5"	0	0	0	0	0	0	0	
Gillnets: 8.0"	0	0	0	0	8	0	0	
Gillnets: >8.0"	0	0	0	0	0	0	0	
Total gillnets	2768	10013	1182	543	2717	1474	1426	
Long line hooks	12438	18123	8180	4280	4318	9950	11575	
Beach seines	6	3	77	0	0	0	0	
Open water seines	167	143	50	14	41	97	36	
Hand line hooks	97	42	19	40	34	99	0	
Open water Dagaa seines	251	92	37	40	25	14	4	
Mosquito nets	0	1	33	0	0	0	0	
Number of traps	0	17	0	0	0	0	19	
Other (unspecified)	0	0	0	0	0	0	0	

4D = Fishing craft with outboard engine for diving for the aquarium fish.

Table 34: Summary of the frame survey results for the whole of the Tanzanian coast of Lake Nyasa.

ITEM	KYELA	LUDEWA	MBINGA	TOTALS
Number of landing sites	25	28	24	77
Number of fishermen	1000	1317	2886	5203
Number of fishing vessels	766	897	1248	2911
Number of outboard engines	0	0	4D	4D
Number of inboard engines	0	0	0	0
Gears by type:				
Gillnets: <1.5"	0	26	330	356
Gillnets: 1.5"	204	141	2621	2966
Gillnets: 2.0"	604	1207	3554	5365
Gillnets: 2.5"	485	2070	6113	8668
Gillnets: 3.0"	391	546	4789	5726
Gillnets: 3.5"	384	220	1440	2044
Gillnets: 4.0"	158	846	1123	2127
Gillnets: 4.5"	236	323	147	706
Gillnets: 5.0"	1182	628	464	2274
Gillnets: 5.5"	8	15	6	29
Gillnets: 6.0"	44	324	106	474
Gillnets: 6.5"	0	3	0	3
Gillnets: 7.0"	0	55	0	55
Gillnets: 7.5"	0	0	0	0
Gillnets: 8.0"	0	139	8	247
Gillnets: >8.0"	0	11	0	11
Total gillnets	3696	6549	20677	30922
Long line hooks	14169	15109	83864	113,142
Beach seines	6	16	86	108
Open water seines	92	267	590	949
Hand line hooks	6	82	375	463
Open water Dagaa seines	76	144	463	607
Mosquito nets	19	12	34	65
Number of traps	257	14	53	324
Other (unspecified)	0	0	0	0

4D = Fishing craft with outboard engine for diving for the aquarium fish.

It is evident (Table 34) it is evident that Mbinga district has the highest number of fishermen, fishing gears and crafts. The table shows a total of 5203 (19.2% from Kyela, 25.3% from Ludewa and 55.5% from Mbinga districts) local fishers exploiting the fish resources of the Tanzanian side of the Lake Nyasa. During the survey aquarium fishers using outboard engines and inflatable or plank boat as diving platforms, were recorded in Mbinga district. But these aquarium fishers sometimes do fish in the other districts. Fish exploitation in the Tanzanian waters is mainly carried out with dugout canoes and the fishers are thus restricted to near-shore. Fishing is carried out using gillnets (<1.5" to 8" mesh size), longlines, open water seine nets for both 'usipa' and the cichlids, handlines and traps are also used. All these are artisanal fishing practices for subsistence and semi-commercial purposes. Large scale purseining and trawling as done in the Malawian side of the lake were not observed in the Tanzanian waters. It is quite unlikely that reliable landing-beach statistics are being recorded by the fisheries department as evidenced from the lack of the necessary beach facilities and in most cases and absence of the fisheries staff.

Fishing craft

All the 2911 dugout canoes (3m – 7m in length) counted during this survey were unmotorized. These primitive fishing crafts restrict the fishermen to fishing mainly in the near-shore. The near-shore areas not only provide breeding platforms but are also nurseries for most of the fishes of Lake Nyasa. Continuous fishing close to shore should be discouraged as it will likely lead to over-fishing in the area. Therefore it is recommended to extend fishing offshore. In order for the fishing effort to extend to the offshore, better and sea-worthy crafts should be encouraged.

Furthermore, fishing communities along the lake rely on the lake as the only media of transport. The road network parallel to the lake-shore is difficult to establish due to the land topography (Livingstone mountain ranges that run parallel and very close to the shore). Therefore the lake-shore communities have to rely on water transport mainly using canoes. Thus the distribution of essential items and services have to be done using dugout canoes. Schools and dispensaries located along the lake get their supplies by use of dugout canoes. Most times when there are bumper catches of fish especially *Engraulicypris sardella* (usipa), *Copadichromis* spp (vituwi), *Diplotaxodon* spp (mamura) and *Rhamphochromis* spp (njerwa) which could easily be dried by fishermen and sold at distant markets, prices are usually low because of transport problems usually exaggerated by bad weather and poor transport crafts. TRC – marine ferry boats only calls in specified villages. In between these villages the use of dugout canoes is the only means of transport. Only Ludewa and Mbinga district councils have each a motorized plank boat that sometime serve their respective lake-shore dispensaries, divisional offices and schools. Three privately own motorized plank boats (2 in Ludewa and one in Mbinga districts) were recorded during this survey. But according to the lake-shore communities, these boats are used for illegal trade of goods with the neighbouring states.

REPORT ON THE 2nd FRAME SURVEY

The 2nd frame survey for Kyela and Ludewa districts took place in the first months of 2002 (including preparation and mobilization of enumerators). The main objective of this second frame survey was to find out if the number of fishermen differ between seasons. Since the seasons for the 3 districts are the same and for logistical reasons, it was not necessary to cover all the three districts.

In all the 3 districts (except Kyela where rains sometime end in late June), the dry spell is in June to early November and the rainy period is November to May. It was therefore imperative that the 1st frame survey was arranged for the month of June/July 2001 (22nd June to end of July 2001 and including identification, mobilization and training of enumerators). The survey covered the same landing sites in all the three districts as reported in the first frame survey report and adopted the same methodology. A total of 17 enumerators (same enumerator except for one location where we had to recruit and training a new enumerator) were involved in this second frame survey.

Tables 5-6 below gives a summary of the results of the second frame survey from the two districts (Kyela and Ludewa). Table 7 compares of the fisheries frame results for the two surveys for Kyela and Ludewa districts. The results reveal that both the number of fishermen, fishing craft and gear change with seasons. For Kyela district which is mainly a flood plain, access by fishermen to the lake becomes difficult as the coastal area is mostly swampy. There is also a dynamic change of livelihoods as most people engage in paddy farming. The coastal area for Ludewa district is characterized by slopes of Mt. Livingstone and therefore farming is mainly subsistence and in most places practiced by women.

Lake Nyasa fish production is higher during rainy season than during the dry season and is dominated by the river migrating cyprinids Mpasu and Mbelele, Opsaridium species (see Catch assessment report). The nearshore waters become more productive (primary production), attracting fish. There is a higher concentration of fishermen in the river mouths during the rainy months than dry seasons.

Table 35: Summary of the results for the second Kyela district fisheries frame survey (EK1-EK8 = Enumerators).

Item	EK1	EK2	EK3	EK4	EK5	EK6	EK7	EK8	Total
Number of landing sites	4	4	3	3	3	2	3	3	25
Number of fishermen	145	162	78	76	150	112	50	74	847
Number of fishing vessels	149	170	34	33	99	73	47	64	669
Number of outboard engines	0	0	0	0	0	0	0	0	0
Number of inboard engines	0	0	0	0	0	0	0	0	0
Gears by type:									
Gillnets: <1.5	0	0	8	5	0	0	0	0	13
Gillnets: 1.5	0	13	10	0	0	0	0	99	122
Gillnets: 2.0	282	45	4	0	38	10	86	211	676
Gillnets: 2.5	14	115	11	5	87	81	155	64	532
Gillnets: 3.0	24	8	16	33	74	35	96	112	398
Gillnets: 3.5	0	8	6	3	197	0	115	10	339
Gillnets: 4.0	54	2	0	0	13	0	58	32	159
Gillnets: 4.5	28	41	6	5	4	0	44	92	220
Gillnets: 5.0	18	158	12	23	528	153	22	300	1214
Gillnets: 5.5	0	0	0	0	0	6	0	0	6
Gillnets: 6.0	0	0	0	0	0	197	0	0	197
Gillnets: 6.5	0	0	0	0	0	0	0	0	0
Gillnets: 7.0	0	0	0	0	0	0	0	0	0
Gillnets: 7.5	0	0	0	0	0	0	0	0	0
Gillnets: 8.0	0	0	0	0	0	0	0	0	0
Gillnets: >8.0	0	0	0	0	0	0	0	0	0
Long line hooks	1880	7560	210	750	380	100	150	1100	12130
Beach seines	0	0	0	0	0	0	1	4	5
Open water seines	0	42	0	0	25	19	2	5	93
Hand line hooks	2	0	6	0	2	0	0	0	10
Open water Dagaa seines	0	34	0	0	18	2	0	3	57
Mosquito nets	0	0	0	0	0	0	0	0	0
Number of traps	72	22	0	0	22	0	2	82	200
Other (unspecified)	0	0	0	0	0	0	0	0	0

EK1 = Ikombe, EK2 = Matema, EK3 = Mwaya I, EK4 = Mwaya II, EK5 = Itungi port EK6 = Kiwira, EK7 = Songwe I and EK8 = Songwe II

Table 36: Summary of the results for the Second Ludewa district fisheries frame survey (EL1-EL9 = Enumerators).

[illegible]

Table 37: Frame survey results for the two surveys done in the dry and wet seasons for Kyela and Ludewa districts (Tanzanian waters of Lake Nyasa).

ITEM	KYELA		LUDEWA	
	July 2001	March 2002	July 2001	March 2002
Number of landing sites	25	25	28	29
Number of fishermen	1000	847	1317	2319
Number of fishing vessels	766	669	897	1129
Number of outboard engines	0	0	0	0
Number of inboard engines	0	0	0	0
Gears by type:				
Gillnets: <1.5"	0	13	26	250
Gillnets: 1.5"	204	122	141	723
Gillnets: 2.0"	604	676	1207	1217
Gillnets: 2.5"	485	532	2070	3316
Gillnets: 3.0"	391	398	546	979
Gillnets: 3.5"	384	339	220	403
Gillnets: 4.0"	158	159	846	1474
Gillnets: 4.5"	236	220	323	752
Gillnets: 5.0"	1182	1214	628	1133
Gillnets: 5.5"	8	6	15	30
Gillnets: 6.0"	44	197	324	353
Gillnets: 6.5"	0	0	3	0
Gillnets: 7.0"	0	0	55	35
Gillnets: 7.5"	0	0	0	0
Gillnets: 8.0"	0	0	139	392
Gillnets: >8.0"	0	0	11	2
Long line hooks	14169	12130	15109	24120
Beach seines	6	5	16	11
Open water seines	92	93	267	375
Hand line hooks	6	10	82	135
Open water Dagaa seines	76	57	144	183
Mosquito nets	19	0	12	0
Number of traps	257	200	14	32
Other (unspecified)	0	0	0	0

Conclusions

The survey revealed several things not previously known:

- For the first time the number of fishermen and fishing vessels and gears has been established in the Tanzanian side of Lake Nyasa.
- That there are no fishermen using motorized boat in the Tanzanian waters of the lake.
- All fishermen in the Tanzanian waters use dugout canoes.
- There is very poor infrastructure in all major fish landing sites.
- For most landing sites and especially in Kyela and Ludewa district there are no fisheries beach recorders and, therefore, the statistical data supplied to the Fisheries Headquarters for planning purposes may not be accurate.
- Most of the gillnets in use are of small mesh size.

The survey highlighted the need to conduct annual frame surveys to monitor the fishing effort.